WINTER FORAGE SELECTION BY BARREN-GROUND CARIBOU: EFFECTS OF FIRE AND SNOW

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WINTER FORAGE SELECTION BY BARREN-GROUND CARIBOU:

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ABSTRACT

Snow depth and hardness were the most influential factors in selection of feeding areas by caribou (*Rangifer tarandus*) in late winter in northwestern Alaska. Following a 1988 fire, plots were established in late March through April in burned and unburned tussock tundra in 1990 and 1991. Snow in both burned and unburned plots was shallower and softer at edges of caribou feeding craters than at adjacent undisturbed points in both years. There was little difference in snow depth or hardness between burned and unburned plots, although caribou cratered in shallower snow in burned plots than in unburned plots in 1990. Crater area was greater in unburned plots in 1990, but there was no difference in crater area between burned and unburned plots in 1991. Frequencies of particular plant taxa were only significant in determining selection of crater sites in unburned plots in 1990, when caribou craters had higher relative frequencies of lichens and lower frequencies of bryophytes than unused areas. Fire reduced relative frequency and biomass of most plant taxa, with the exception of post-disturbance species, which occurred primarily in burned plots. Lichens were reduced in burned plots, and lichens composed 59-74% of the late-winter diet of caribou, as determined by microhistological analysis of fecal pellets. Biomass and relative frequency of *Eriophorum vaginatum* was greater in burned plots than in unburned plots in 1991, and protein and *in vitro* digestibility levels were enhanced in samples of this species collected from burned plots in late winter.

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INTRODUCTION

Debate over the role of wildfire in the ecology of barren-ground caribou (*Rangifer tarandus)* has generated both questions and controversy. Disagreement is centered on whether effects of fire are detrimental or beneficial on winter range of caribou. Access to forage in winter is restricted by snow, which limits its availability and increases energy expenditure involved in traveling and feeding. Fire can further hamper foraging caribou by removing plant biomass and thereby reducing the quantity of forage available. Lichens, often the primary food for caribou in winter, are easily destroyed by fire (Scotter 1964). The species of lichens preferred by caribou and reindeer have been characterized as 'old-growth' species, and 30 to 100 years or more may be needed following fire for lichens to regain previous, or at least usable, levels of abundance (Palmer 1941, Skuncke 1969, Scotter 1971, Viereck 1973, Pegau 1975). This long-term reduction in availability of winter forage following fire has been proposed as being responsible for previous declines in caribou numbers in Alaska and Canada (Leopold and Darling 1953, Edwards 1954, Kelsall 1960, Scotter 1967, Pruitt 1978). Conversely, fire plays a role in creating and maintaining vegetative heterogeneity that is important for the long-term productivity of caribou (Miller 1974, 1980, Klein 1982, Schaefer and Pruitt 1991).

Snow Cover

Snow cover has been cited as the primary determinant of foraging patterns of caribou in winter (White et al. 1981, Miller et al. 1982), and populations of arctic ungulates may be limited more by snow characteristics than by the amount of forage available beneath the snow (Henshaw 1968, Reimers 1977, Parker 1978, Gates et al. 1986). Estimates of availability of ground forage to caribou in winter varies between 1 and 5% of the total forage present (Bergerud 1974a, Adamczewski et al. 1988), and considerable energy may

be expended while caribou search for accessible forage (Helle 1984). Digging or 'cratering' through the snowpack to reach vegetation involves additional energetic costs, and it may not be efficient to crater in snow that is excessively deep or hard.

Caribou crater in snow that is shallower and softer than surrounding undisturbed areas (Biddlecomb 1992), presumably to reduce the energetic costs of foraging (Fancy and White 1985). Snow deeper than 50-70 cm may hinder caribou and reindeer movements and digging (Pruitt 1959, Henshaw 1968, La Perriere and Lent 1977, Brooks and Collins 1984, Adamczewski et al. 1988). Craters tend to occur in snow that is 10 - 25 cm deep (Skogland 1978, Miller et al. 1982, Thomas and Edmonds 1983). Cratering activity by caribou and reindeer apparently is stimulated by the sight (Miller et al.1982, Bergerud 1974a) and scent (Nasimovich 1955, Helle 1984) of forage plants. Caribou are able to smell forage beneath 15-18 cm of undisturbed snow and may detect forage under deeper snow if air passages formed by vegetation are present (Bergerud 1974a). Deep snow may hinder detection of, as well as access to, food.

Values of snow hardness that potentially impede cratering by *Rangifer* vary with factors such as habitat and season (Skogland 1978), and range from 85 g/cm^2 in the taiga (La Perriere and Lent 1977) to 9,000 g/cm^2 in the tundra (Thing 1977). Others estimate that hardness values between 22,000-29,000 g limit cratering activity (Skogland 1978, White et al. 1981).

Winter Forage

The dependence of most continental populations of caribou on terrestrial lichens is well documented (Pegau 1968, Miller 1974,1976, Klein 1980, 1982, Miller et al. 1982, Adams 1983, Vandal and Barrette 1984, Hinkes and Campbell 1984, Russel and Martell 1984, Fleischman 1990, Schaefer and Pruitt 1991). Fluctuations in caribou and reindeer populations have been associated with changes in lichen availability (Gaare and Skogland

1980), and low biomass or poor access to lichens, accompanied by extreme weather conditions, is implicated in population crashes of *Rangifer* (Klein 1968, Reimers 1977, Skogland 1986). Although low in crude protein (approximately 2-5%; Parker 1975, Miller et al. 1982), lichens contain high levels of starch, are easily digested by caribou and reindeer, and are a source of available energy (Skuncke 1969, Klein 1970, 1982). Dry matter digestibility of some lichens by caribou is estimated to be approximately 70% (Thomas and Kroeger 1980, White et al. 1981).

Winter-green vascular plants can be an important supplement in the winter diet of caribou subsisting primarily on lichens (Skuncke 1969, Parker 1975, Miller 1976, Thomas and Kroeger 1980, Klein 1982, Helle and Tarvainen 1984, Helle 1984, Russel and Martell 1984). Pregnant reindeer, fed additional protein and minerals with a lichen diet, gained weight (Jacobsen and Skjenneberg 1975, Jacobsen et al. 1981, Rognmo et al. 1983), yielded increased quantities of milk, and their calves had accelerated rates of growth (Jacobsen and Skjenneberg 1975, Jacobsen et al. 1981). In addition, protein supplements were correlated with significant increases in the voluntary intake of lichens by reindeer (Jacobsen and Skjenneberg 1975, Jacobsen et al. 1981), and digestibility of lichens was enhanced when nitrogen was added (Trudell et al. 1980).

Fire Effects

Despite its effects on lichen availability, fire in northern ecosystems may potentially benefit caribou by enhancing the productivity and nutritive status of vascular plants (Scotter 1972, Viereck 1973, Johnson and Rowe 1975, Kelsall et al. 1977, Johnson 1981, Klein 1982). In northern systems, burning commonly results in short-term increases in the concentration of nutrients in soil and ash layers (Viereck and Schandelmeier 1980, MacLean et al. 1983) and in plant tissue (Racine 1979). Elevated availability of light, nitrogen, and phosphorus stimulate growth in most arctic plants, although the extent to

which growth is increased is variable (Shaver and Kummerow 1992). Nitrogen often limits the productivity of vascular plants in northern ecosystems (Ulrich and Gersper 1978, MacLean et al. 1983, Lent and Klein 1988, Nadelhoffer et al. 1992) and it is also an important component of herbivore diet (Mattson 1980, Klein 1981). Burning can result in significant losses of nitrogen via volatilization when sufficiently high temperatures are achieved (MacLean et al. 1983, Viereck 1983). In northern systems, enhanced levels of nitrogen in post-fire vegetation are largely a result of increased rates of organic matter mineralization due to heightened soil temperatures (Dubrevil and Moore 1982). Lowered surface albedo and removal of vegetative insulation following fire increase soil temperatures early in summer (Scotter 1971,Wein and Bliss 1973, Haag and Bliss 1974, Kershaw et al. 1975, Kershaw 1977, Viereck and Schandelmeier 1980), and warmer soils increase the activity and numbers of soil microorganisms, thereby speeding decomposition processes and mobilizing nutrients for use by plants (Lutz 1956, MacLean et al. 1983). This release of nutrients can be especially important where cold temperatures normally slow decomposition rates, and many nutrients are tied up in organic matter (MacLean et al. 1983). Phosphorus (Lutz 1956, Wein and Bliss 1973, Racine 1979), potassium (Lutz 1956, Wein and Bliss 1973, Racine 1979, Viereck 1983), and magnesium (Wein and Bliss 1973) concentrations also may increase after fire. It is questionable whether this increase in nutrient availability likewise benefits lichens (Skuncke 1969), which extract mineral nutrients from precipitation (Hale 1967).

The presence of permafrost restricts availability of nutrients to plants because nutrients must be extracted from the 'active layer' of thawed soil. Warmer soil temperatures following fire cause deeper melting and a thicker active layer (Mackay 1970, Hall et al. 1978, Viereck and Schandelmeier 1980, Racine 1981, Brown 1983, MacLean et al. 1983, Racine et al. 1987), thereby increasing the volume of soil from which plants can obtain nutrients (Wein and Bliss 1973). Fetcher et al. (1984) reported that a significant difference

in the average depth of thaw between burned and unburned areas persisted 13 years following a fire in tussock tundra. The active layer in forest tundra near Inuvik, Canada, increased by greater than 50 cm over an 8 year period, with rapid thickening during the first 4 to 5 years and only a minor increase at 8 years (Brown 1983).

Fires play a role in altering or maintaining the character of plant communities, the results of which may be useful to wildlife. Many species of wildlife primarily occur in early successional habitats created by large-scale disturbance, such as fire. The pattern of succession after burning is dependent on a number of factors, including the composition of the original community, fire intensity, and previous fire history (Miller 1980). Succession occurs within lichen communities as well as in higher plant communities, and there are distinct seral stages of mosses and lichens (Kershaw 1977, Black and Bliss 1978, Pegau 1970, Lawrey 1991). Although post-fire succession in the taiga has been well documented (Viereck and Schandelmeier 1980, Johnson 1981, Foote 1983, Viereck 1983), the patterns of recovery following tundra fires are not as well known. Until recently, few data were available on the effects of tundra fires because they were considered rare events and there was little evidence of previous fires, such as fire scars and other dendrochronological clues (Viereck and Schandelmeier 1980). Tundra fires are more common than once believed, however, and there is a growing awareness of their importance to the tundra ecosystem (Auclair 1983, Racine et al. 1987). Racine (1981) reported that tussock tundra, commonly used by caribou in early spring (Roby 1978, Kuropat and Bryant 1980, Wright 1980, Davis et al. 1982), was the vegetation type least affected by fire in terms of changes in thaw depth and post-fire vegetative composition, whereas dwarf shrub tundra (birch and ericaceous shrubs) was the most severely affected. Low ericaceous shrubs have a high susceptibility to fire because of their chemical constitution and growth form, which provides a near-continuous cover of potential fuel (Auclair 1983). Cover of vascular plants in tussock tundra may regain pre-fire levels within 6-10 years after burning (Racine et al.

1987), and tussock tundra may require periodic burning to prevent paludification or dominance of other plant species (Racine 1979, 1981, Viereck et. al. 1992). Although vegetative cover and productivity may be reestablished relatively quickly after fire, restoration of pre-fire abundance of some species, notably lichens, may take much longer (Fetcher et al. 1984). The recovery of lichens is particularly slow because the average growth of lichens used by caribou may be < 5 mm per year (Andreev 1954, Scotter 1964, Pegau 1968). Sources for the recolonization of lichens may be limited, although fragments and soredia (Armstrong 1991) from surviving lichens in the burn or in unburned islands are potential sources for lichen recolonization.

Although fire plays a prominent role in the winter ecology of caribou in forested areas, little information is available concerning the effects of tundra fire on caribou. Most continental populations of caribou winter on forested ranges that have evolved with fire. Some caribou, however, spend winter on tundra ranges, and even those that migrate to the taiga may eventually cross snow-covered expanses of burned tundra. In addition, herded reindeer may be restricted to tundra ranges throughout the year (L. Renecker, pers. comm.) and their herders could profit from increased information on the consequences of tundra fires for reindeer, whether they are primarily using lichens or winter-green vegetation. Few studies, however, have examined the consequences of tundra fires on caribou and reindeer.

I hypothesize that caribou feeding patterns in burned and unburned habitat in late winter are determined by snow and vegetation characteristics. Given this hypothesis, I predict that the following conditions will occur. Cratered sites will have shallower, softer snow than adjacent uncratered sites and snow depth and hardness will differ between burned and unburned plots. Cratered sites will contain lower amounts and different types of vegetation than adjacent uncratered sites, and burned plots will contain different amounts and types of vegetation than unburned plots. Forage quality will be enhanced in burned plots, and caribou winter diet will differ between recently burned and unburned areas.

STUDY AREA

The Selawik National Wildlife Refuge (SNWR) is located east of Kotzebue Sound in northwestern Alaska and lies between the Waring Mountains to the north and the Selawik Hills to the south (Fig. 1). Portions of the northern and southern borders abut Kobuk Valley National Park and the Koyukuk National Wildlife Refuge, respectively. The villages of Noorvik and Selawik are located within the refuge boundaries, and residents use the refuge for subsistence purposes. Bisected by the Arctic Circle, the refuge encompasses 849,858 ha, which includes a 97,127-ha wilderness area in the northern portion. The refuge contains many different habitat types including alpine and arctic tundra, wetlands, beaches and sand dunes.

The Waring Mountains fire (Fig. 1) burned in the northeast portion of SNWR from 15 June to mid-August 1988. Refuge policy permitted fires to burn if they did not endanger life or property (U.S. Fish and Wildlife Service 1987). The fire initially was reported in a limited suppression area, and there were no suppression efforts until 16 June when native allotments were threatened and the fire had already burned 2,428 ha. By late June, the fire had burned mostly black spruce (*Picea mariana*) and muskeg on lower portions of the Waring Mountains, but by 12 July the fire had spread southwards into wetlands and east into habitat of migrating caribou (Jerry et al. 1988). Although the fire was largely continuous for over 84, 984 ha (Jerry et al. 1988), a fire mosaic was formed because fire intensity varied with weather conditions, vegetation type, and moisture regimes (Racine 1979).

The fire burned areas of the refuge historically used as a migration corridor and occasional winter range by caribou of the Western Arctic Herd (WACH). The herd occupies the northwest quarter of Alaska, ranging between 65° to 71°N latitude and 148°

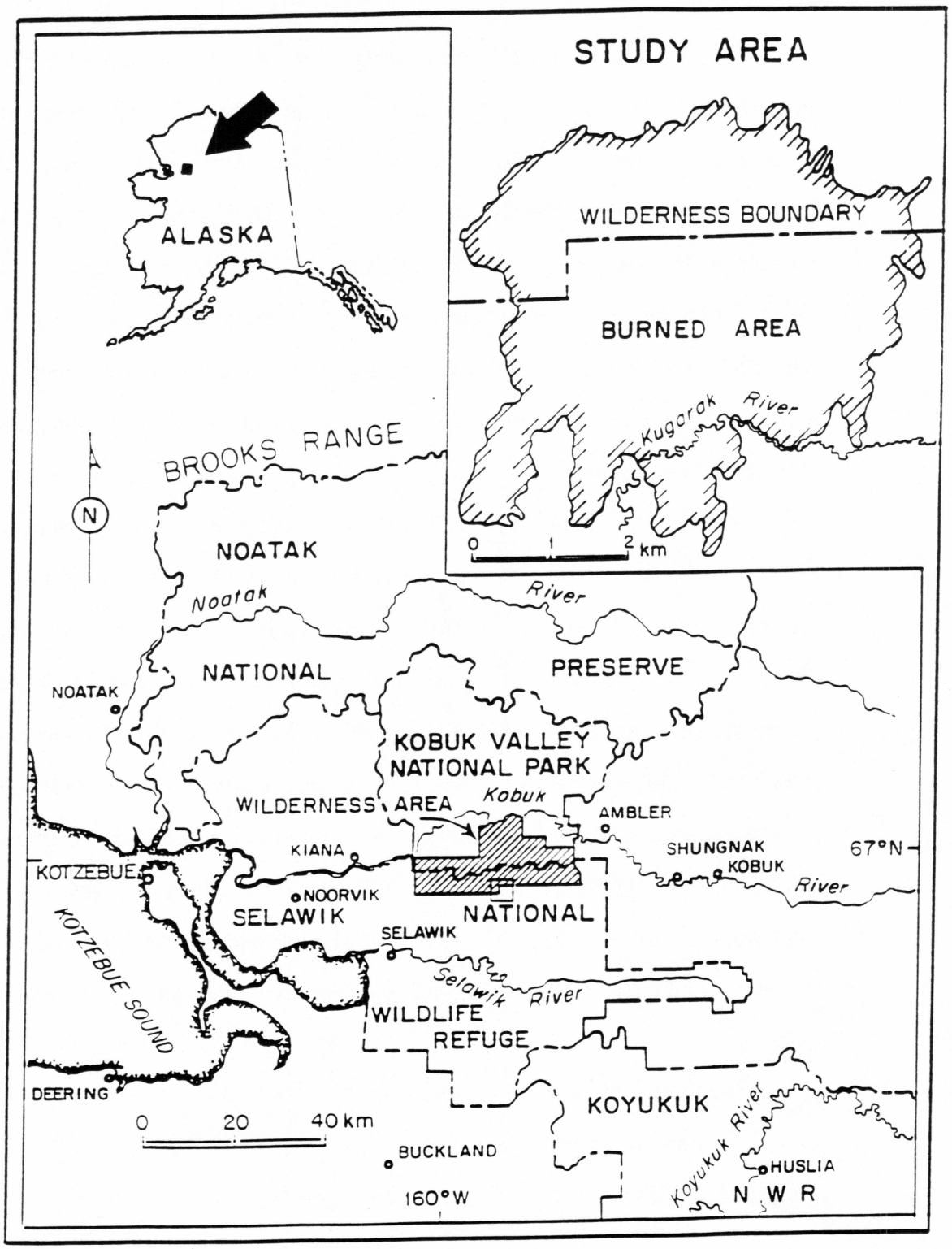

Fig. 1. Location of the general study area in Selawik National Wildlife Refuge and its relationship to the Waring Mountains Burn.

to 166.30°W longitude (Davis et al. 1980). Current estimates of population size place the herd at a minimum 415,700 (J. Dau 1993, pers. comm.). The WACH generally calves in the Utukok drainage north of the Brooks Range and winters in the Buckland Valley, Nulato Hills, and other areas (Spindler 1989). Although few caribou spend the winter on the refuge, up to 32% of the herd may be present at any given time during spring and autumn migrations (Robinson and Spindler 1989).

The area chosen for this study consists of tussock-shrub flatlands along the Kugarak and Selawik Rivers. The topography of the study area is relatively flat (≤ 16 m elevation) interrupted with small rolling hills (usually < 46 m elevation). Wetlands and bogs are abundant, ranging in size from small 'pothole' ponds to large lakes (≥ 1 km^2). The tops of ridges and hills tend to be drier than surrounding low-lying areas. Most of the study area is composed of tussock tundra with some plots located in open, low mixed shrub-sedge tussock tundra, as described by Viereck et al. (1992). Vegetation consists of dwarf shrubs (primarily *Ledum palustre*, *Vaccinium* spp., and *Betula nana*), graminoids (mostly *Carex* spp. and *Eriophorum* spp.), lichens and forbs. Grasses are present in burned areas but rarely occur in unburned habitat. Trees (*Picea glauca* and *P. mariana*) and taller shrubs (*Salix* spp. and *Alnus crispa*) occur in riparian areas and around larger lakes. A list of plant species occurring in plots is included in Appendix 1 (Hulten 1968, Moberg and Holmasen 1982, Thomson 1984). Unvegetated expanses of burned ground were encountered in burned areas, particularly in 1990. I selected this site because caribou reportedly use this area during spring migration on a regular basis (Spindler 1989) and both burned and unburned areas were accessible by river.

METHODS

Plot Selection

Study plots (30 by 30 m), each containing cratered and undisturbed snow, were established between 6 April and 1 May 1990 in both burned (n=20) and unburned (n=20) areas; between 27 April and 3 May 1991, 16 plots were located in both burned and unburned areas (Fig. 2). In 1991, there were only eight days between the arrival of caribou and breakup, when melting snow and ice make travel via snowmobiles difficult. Winter field seasons in both years ended with the onset of breakup. Craters were located from the air when possible or by following caribou trails. Craters usually were located on level ground or on low ridgetops and I attempted to space plots at least 0.4 km apart. Plots were randomly oriented with respect to direction and distance from edges of craters. Plot locations were mapped on 1:63,360 topographical maps and three corners of the plot were marked by hammering 0.5 m sections of hollow pipe into the frozen ground and inserting 1.4 m tall fiberglass poles. Ten points were located in undisturbed areas within each plot. These random points, and the least disturbed edges of craters ('cratered points') were sampled for snow depth and hardness using a Rammsonde Penetrometer, which measures the resistance of the snowpack to penetration (Lent and Knutson 1971, Skogland 1978, Duquette 1988). Data were pooled to provide one mean value for depth and hardness per plot. Area of craters in each plot was determined from scale maps of plots drawn on graph paper and used as an index of cratering effort by caribou.

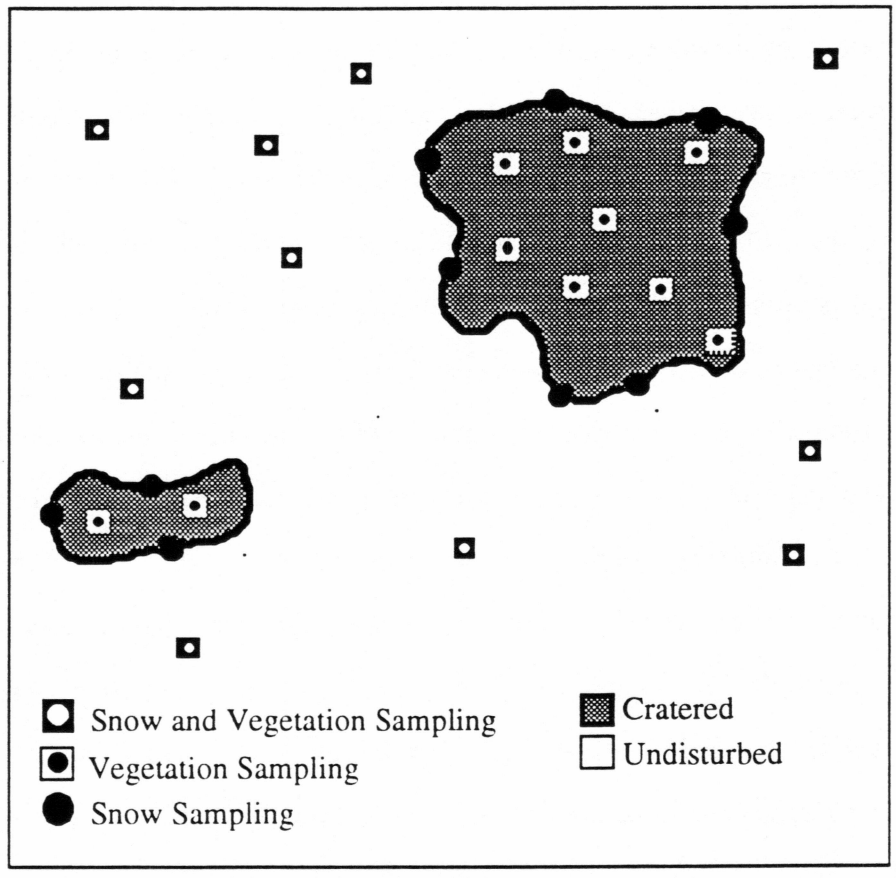

Fig. 2. Schematic diagram of plot design for sampling snow and vegetation in northwestern Alaska.

Late-Winter Diet Composition

Caribou fecal pellets were collected throughout the winter field season in each year and analyzed at the Wildlife Habitat Lab at Washington State University to provide an index of diet composition. Fecal samples consisted of one composite sample each from burned and unburned habitat. Plant epidermal fragments were microhistologically identified to major forage genera, and cover values of fragments were used to determine the percent diet composition (Davitt and Nelson 1989). Cover values were calculated from 150 microscope views of fecal material. Different forage species may be under or over estimated in fecal analysis depending on the degree of digestibility (Dearden et al. 1975, Boertje et al. 1985), so a correction formula using different *in vitro* digestibilities by caribou was derived using data from Boertje (1981). The formula is as follows, with calculated values reapportioned so that total diet composition equals 100%:

$$\frac{\text{Uncorrected cover value from fecal analysis}}{\text{1-\% Dry Matter Digestibility from Boertje (1981)}}$$

Late Winter Forage Quality

Above-ground vegetation was collected from craters in burned and unburned plots prior to breakup in late April of each year, separated by species, and divided into current and previous years' growth. This was analyzed for fiber composition (ADF, NDF, and ADL; Van Soest sequential fiber analysis), *in vitro* dry matter digestibility, and protein content (% crude protein=% Kjeldahl nitrogen x 6.25) (Van Soest 1982). In the sequential fiber analyses, cell solubles were calculated as 1-%NDF (neutral detergent fiber), hemicellulose as %NDF-%ADF (acid detergent fiber), %ADF-%ADL (acid detergent lignin) measured cellulose, and ADL was a measure of indigestible lignin (Person et al. 1980, Robbins 1983).

In vitro digestibility (Goering and Van Soest 1970) was determined using cow rumen fluid and may differ from actual digestibility by caribou. Moreover, these measures

provide no information about the presence of secondary compounds, which may affect palatability and ingestion (Person et al. 1980). Nonetheless, these digestibility values do provide a useful index for comparing vegetation between burned and unburned craters. I used a regression formula employing NDF to predict dry matter digestibility of lichens in summer (Person et al. 1980) if caribou were inoculum donors. The formula is as follows:

In vitro Dry Matter Digestibility=53.4 - 0.07(NDF).

In vitro digestibility was not calculated for *E. vaginatum* from burned plots in 1990 due to insufficient material. To compare digestibility of *E. vaginatum* between burned and unburned plots, I used a formula regressing nitrogen content to *in vitro* digestibility of graminoids (Kuropat 1984; Digestibility=32.53 + 8.26 N). In 1990, samples of each species collected from different plots were combined into one composite sample for each species. This composite sample and one replicate lab sample of the plant material listed in Table 1 were analyzed. In 1991, four to five samples of each species in Table 1 were analyzed.

Crater Density

Four transects, each approximately 50 km in length and containing both burned and unburned habitat, were flown in late April of both years to estimate the density of feeding areas. A feeding area was defined as cratered snow separated from other cratered areas by a patch of undisturbed snow. In 1990, transect width was estimated between 0.4 to 0.8 km and results are reported as the number of feeding areas per linear kilometer. In 1991, the airplane struts were marked to delineate a transect width of 0.4 km and results are reported as the number of feeding areas detected per square kilometer.

Table 1. Plant taxa collected from burned and unburned habitats in northwestern Alaska, 1990 and 1991, that were analyzed for fiber and nutrient content.

Year	Plant	Plots collected from*
1991	Charred lichen	B
	Unburned lichen	UB
	Eriophorum vaginatum (leaves)	B and UB
	E. vaginatum (standing dead)	B and UB
	Grasses	B
	Vaccinium vitis-idaea (leaves)	UB
1991	Lichen	UB
	E. vaginatum (leaves)	B and UB
	V. vitis-idaea (leaves)	B and UB

* B=Burned, UB=Unburned.

Summer Sampling

During 10-30 July 1990 and from 26 June to 8 July 1991, quadrats measuring 0.25 by 0.25 m were established on the 10 random points sampled in April and on 10 points randomly located within former craters in burned and unburned plots. I was able to locate all plots but one burned plot in 1990. Species lists were compiled for each quadrat and the percent relative frequency (Kershaw 1964) for major species of interest in a plot was calculated as:

$$\% \text{ Relative frequency species A} = \frac{\text{Number of quadrats per plot containing species A}}{\text{Sum of frequency values of all species in plot}} \times 100$$

For example, if a plot contained 4 plant species with species A occurring in 3 quadrats, and species B, C and D occurring in 4, 7, and 8 quadrats, respectively, the relative frequency of species A would be:

$$\% \text{ Relative frequency species A} = 3 \div (3+4+7+8) \times 100$$

All above-ground vegetation, except for bryophytes, was clipped in five of the random quadrats in each plot to estimate biomass. Biomass measurements were not collected from craters because the quantity of vegetation actually removed by caribou was unknown. Vegetation was sorted into current and previous years' growth (Shaver and Chapin 1991), dried at 60° C for 24 h, and weighed to the nearest 0.01 g. Lichens were separated into different categories of preference by caribou. Vegetative biomass from the five quadrats were averaged by species for each plot.

Statistical Analyses

Each year was analyzed separately because mean snow hardness differed between years. These data were ranked prior to analysis due to nonnormal distributions (Zar 1984). Step-wise discriminant function analysis (DFA, forward selection and backward elimination; SAS Institute 1989) was used to select key variables prior to performing

statistical tests. Class variables used in the step-wise analysis were burn (burned vs. unburned) and use (random vs. cratered). The percent of quadrats placed into correct burn and use categories was determined by *a posteriori* tests in DFA. Linear discriminant functions were used where equality of the covariance matrices occurred; if this assumption was not met, quadratic functions were employed. Because some assumptions concerning multivariate normality may have been violated, discriminant analysis was of an exploratory rather than a comfirmatory nature (Williams 1983, Edge et al. 1988). Data on snow and relative frequency of plants were analyzed using multiple analysis of variance (MANOVA). Independent variables were fire history (burned vs. unburned) and use (cratered vs. random), and dependent variables were the snow and vegetation variables selected by step-wise DFA. The MANOVA tested for overall differences due to recent fire history, use, and the interaction between fire history and use. In the model for the MANOVA, plots were nested within burn type, there was a burn by use interaction, and the plot by use interaction was nested within burn type. Plot by use nested within burn type was used as the error term. When using a designated error term in performing MANOVAs with SAS, F-statistics and probabilities are provided for the overall effects but not for each dependent variable. Thus, the effects on individual dependent variables were evaluated using ANOVAs similar to those recommended for a split-plot model (SAS Institute 1989).

A Mann-Whitney U-test (Zar 1984) was used to determine if there were differences in crater size between burned and unburned plots. Mann-Whitney U-tests also were used to test for differences due to burning in fiber and nutrient content and digestibility of plant samples collected in April 1991. Fiber, nutrient, and digestibility analyses in 1990 were performed on vegetation from one composite sample for each species, thus no statistical analyses were performed. Although fecal pellets from burned and unburned habitats were analyzed separately, the results of the microhistological tests were combined because pellets from one habitat may contain material eaten in another. These data are presented for

descriptive purposes only. Transect data were analyzed using the Wilcoxon test (Zar 1984). Vascular plant biomass was divided into the following categories: evergreen shrubs, deciduous shrubs, sedges, grasses, and forbs (including *Equisetum* spp.). Lichens were divided into categories of high, moderate, and little or no use by caribou and were analyzed separately from green vegetation. Mann Whitney U-tests were used to analyze differences in biomass between burned and unburned plots.

RESULTS

Variable Selection

In 1990, variables selected by the stepwise discriminant function analysis (DFA) to distinguish between burned and unburned plots were mean snow depth and hardness and the mean relative frequencies of occurrence of *Empetrum nigrum, Betula nana, Vaccinium uliginosum*, lichens in the genera *Cetraria*, *Cladina*, *Cladonia*, and *Peltigera*, and bryophytes (Table 2). *E. nigrum*, *B. nana*, and *V. uliginosum* were subsequently dropped from the analyses because although frequencies of these species distinguished between burned and unburned plots, they are not important winter forage for caribou and did not enable separation of cratered and random areas as did snow depth, snow hardness, lichens, and bryophytes. In 1991, the variables selected by stepwise DFA to distinguish between burned and unburned plots were mean snow depth and hardness, and the mean relative frequencies of lichens, bryophytes, and *Eriophorum vaginatum*. (Table 2). Although *E. vaginatum* was not selected by stepwise DFA in 1990, it was included in ANOVAs for comparison between years. Snow depth and hardness were selected as the only influential variables determining whether an area would be cratered.

Table 3 presents the standardized canonical correlation coefficients derived from the discriminant function analysis, and positive values indicate selection of a variable by caribou, whereas negative values indicate avoidance (Table 3). A high percent (range=68-100%) of the quadrats were correctly placed in the appropriate burn and use categories by DFA in both years (Table 4).

Table 2. Variables selected by stepwise discriminant analysis from data collected in northwestern Alaska in late winter and summer, 1990 and 1991.

Year	Class categories[1]	Variables selected by stepwise DFA[2]	F-value	Partial r^2
1990	Burned vs	Lichens	73.083***	0.4902
D.F.=1, 76	Unburned	*Betula nana*	12.707***	0.1449
		Vaccinium uliginosum	4.317*	0.0551
		Snow depth (cm)	7.917**	0.0978
		Empetrum nigrum	5.921*	0.0760
	Cratered vs	Snow depth (cm)	29.272***	0.2781
	Random	Snow hardness (kg)	7.383**	0.0896
		Bryophytes	5.601*	0.0704
1991	Burned vs	Lichens	21.060***	0.1432
D.F.=1, 126	Unburned	Bryophytes	35.802***	0.2226
		Eriophorum vaginatum	5.087*	0.0394
	Cratered vs	Snow depth (cm)	166.508***	0.5692
	Random	Snow hardness (kg)	9.957**	0.0738

[1] Separate tests performed for different class categories

[2] Vegetation variables were reported as the % relative frequency of occurrence, and variables are listed in their order of selection. *Betula nana, Vaccinium uliginosum, and Empetrum nigrum* were dropped from subsequent analyses.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 3. Pooled within-class standardized canonical correlation coefficients from DFA for variables from cratered and random quadrats in burned and unburned plots, northwestern Alaska, 1990 and 1991.

Year	Variable[1]	Fire history[2]	Cratered vs Random[3]
1990	Snow depth (cm)	B	-0.926
D.F.=4, 33		UB	-0.640
	Snow hardness (kg)	B	-0.178
		UB	-0.738
	Bryophytes (%)	B	-0.270
		UB	-0.042
	Lichens (%)	B	0.023
		UB	0.431
1991	Snow depth (cm)	B	-0.978
D.F.=5, 26		UB	-1.192
	Snow hardness (kg)	B	-0.267
		UB	-0.363
	Bryophytes (%)	B	0.071
		UB	0.002
	Lichens (%)	B	0.447
		UB	0.017
	Eriophorum vaginatum (%)	B	0.695
		UB	0.005

[1] Snow data was collected in late winter and vegetation data was collected in summer. Sample sizes: 1990, n=20 burned, 20 unburned in winter; 19 burned and 20 burned in summer; 1991 n=16 burned, 16 unburned winter and summer.

[2] Data was divided by plot type (B=burned, UB=unburned); use type, random vs cratered, was used as the class variable.

[3] Negative values indicate avoidance by caribou, positive values indicate selection.

Table 4. Percent of plots in northwestern Alaska correctly classified into burn categories and categories of caribou use by discriminant analysis using variables selected by stepwise procedure.*

Year	Burned		Unburned		Cratered		Random	
	Cratered	Random	Cratered	Random	Burned	Unburned	Burned	Unburned
1990	89	68	85	95	84	100	89	100
1991	94	100	87	87	81	100	94	100

* Variables and sample sizes are the same as in Table 3.

Snow Characteristics and Plant Relative Frequency

Overall, there were significant differences in the selected variables between burned and unburned plots in both years, and caribou selected crater sites on the basis of different snow and vegetative characteristics (MANOVA, Table 5). The interaction between burning and use, however, was not significant in either year (Table 5). ANOVAs, employed to indicate which variables contributed to the overall differences observed in the MANOVA, indicated that caribou cratered in snow that was significantly softer and shallower than snow at random points in both burned and unburned plots in both years (Table 6, Fig. 3). Caribou selected crater sites on the basis of plant relative frequency only in unburned plots in 1990. These craters had a higher relative frequency of lichens and a lower relative frequency of bryophytes in summer than random quadrats (Fig. 4). Neither were there differences in plant relative frequencies between cratered and random quadrats in burned plots in 1990, nor did relative frequencies differ between cratered and random quadrats in burned or unburned plots in 1991 (Table 6, Fig. 4). The canonical correlation coefficient for bryophytes was positive in 1991 (Table 3), indicating preference, but caribou did not crater in areas with high relative frequencies of bryophytes in 1990. The coefficients in 1991 are small, however, and any positive trend is likely negligible.

Differences in snow and vegetation variables also were detected between burned and unburned plots (Table 7). Caribou cratered in shallower snow in burned plots than in unburned plots in 1990 (Fig. 3), but because snow depth did not differ between burned and unburned random points it appears that burning itself did not affect snow cover, but caribou actively cratered in shallower snow in the burn. Snow was softer at unburned random points compared with burned random points in 1991, but this difference was not significant (P=0.0731, ANOVA, Fig. 3, Table 7). Lichens were detected at

Table 5. Results of MANOVAs analyzing differences between burned and unburned plots and between cratered and undisturbed quadrats in northwestern Alaska, 1990 and 1991.

Year[1]	Effect	Hotelling-Lawley trace	F-value
1990	Burned vs Unburned	1.578	13.412***
D.F.=4, 34	Cratered vs Random	0.807	6.863***
	Burning*Use	0.126	1.069 NS
1991	Burned vs Unburned	1.357	7.058***
D.F.=5, 26	Cratered vs Random	2.645	13.755***
	Burning*Use	0.174	0.9028 NS

[1] Variables entered in 1990 were snow depth and hardness and the percent relative frequencies of lichens and bryophytes. In 1991, variables were snow depth and hardness and the percent relative frequencies of lichens, bryophytes, and *Eriophorum vaginatum*.
* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, NS=not significant.

Table 6. F-values derived from ANOVAs comparing random areas and areas cratered by caribou in northwestern Alaska, 1990 and 1991.

Year	Variable[1]	Fire history[2]	F-value (Cratered vs Random)
1990	Snow depth (cm)	B	24.97***
		UB	13.18***
	Snow hardness (kg)	B	4.65*
		UB	13.35***
	Bryophytes	B	0.81 NS
		UB	5.68*
	Lichens	B	0.58 NS
		UB	7.21*
	ERVA[3]	B	0.42 NS
		UB	1.18 NS
1991	Snow depth	B	78.77***
		UB	23.01***
	Snow hardness (kg)	B	12.43*
		UB	4.99*
	Bryophytes	B	1.37 NS
		UB	0.72 NS
	Lichens	B	0.00 NS
		UB	0.58 NS
	ERVA	B	0.21 NS
		UB	0.02 NS

[1] Vegetation variables are expressed as % relative frequency of occurrence.
[2] B=Burned, UB=Unburned.
[3] ERVA=*Eriophorum vaginatum*. ERVA was not selected by the stepwise procedure or entered in the MANOVA in 1990; it is included here for descriptive purposes.
* P≤0.05, ** P≤0.01, *** P≤0.001, NS=not significant.

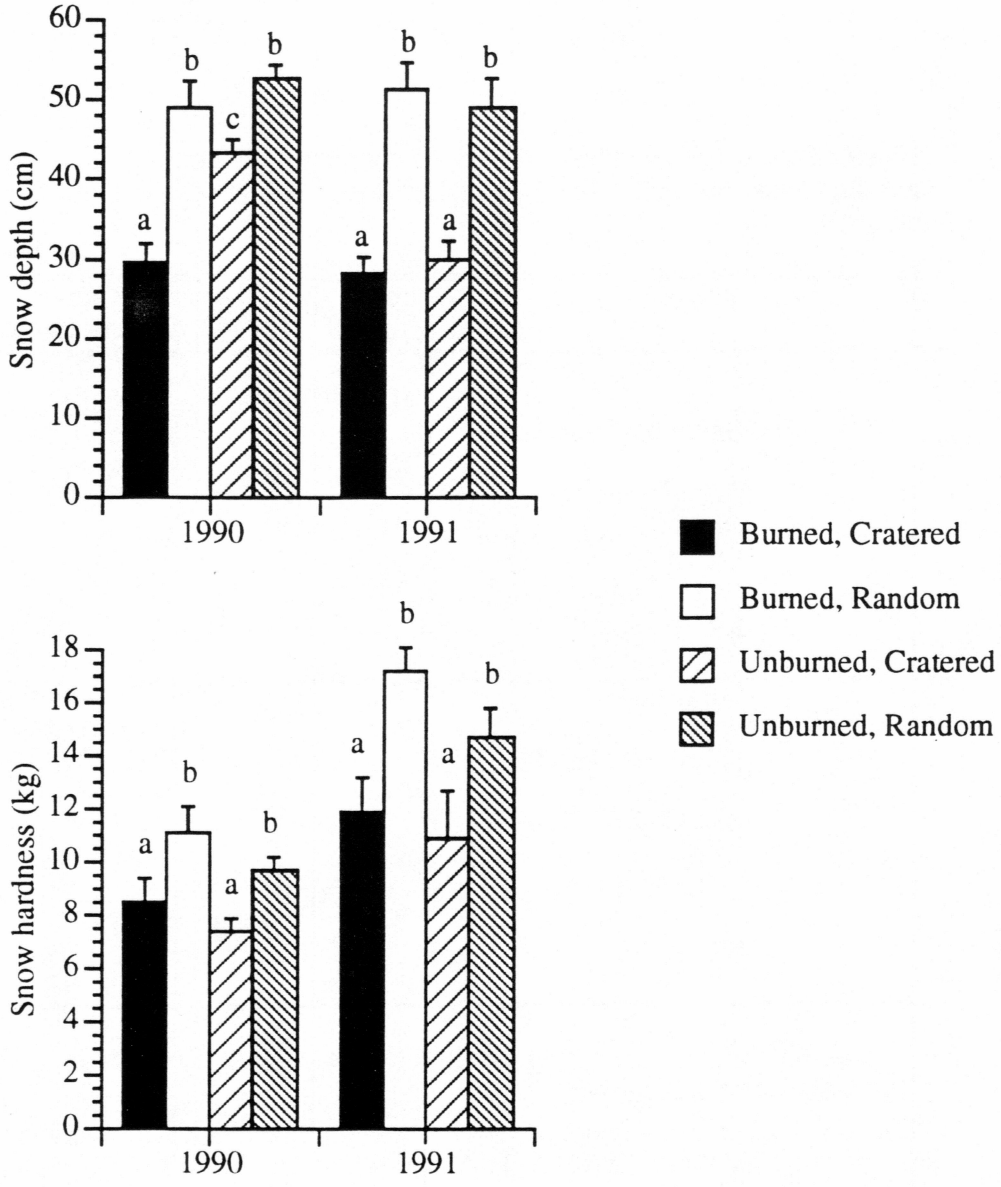

Fig. 3. Mean snow depth and hardness (+SE) occurring at the edges of caribou craters and at randomly located unused points in burned and unburned habitat in northwestern Alaska, 1990 and 1991.

Different letters above bars indicate significant differences within a year.
In 1990 burned plots n=20, unburned plots n=20; in 1991burned plots n=16, unburned plots n=16.

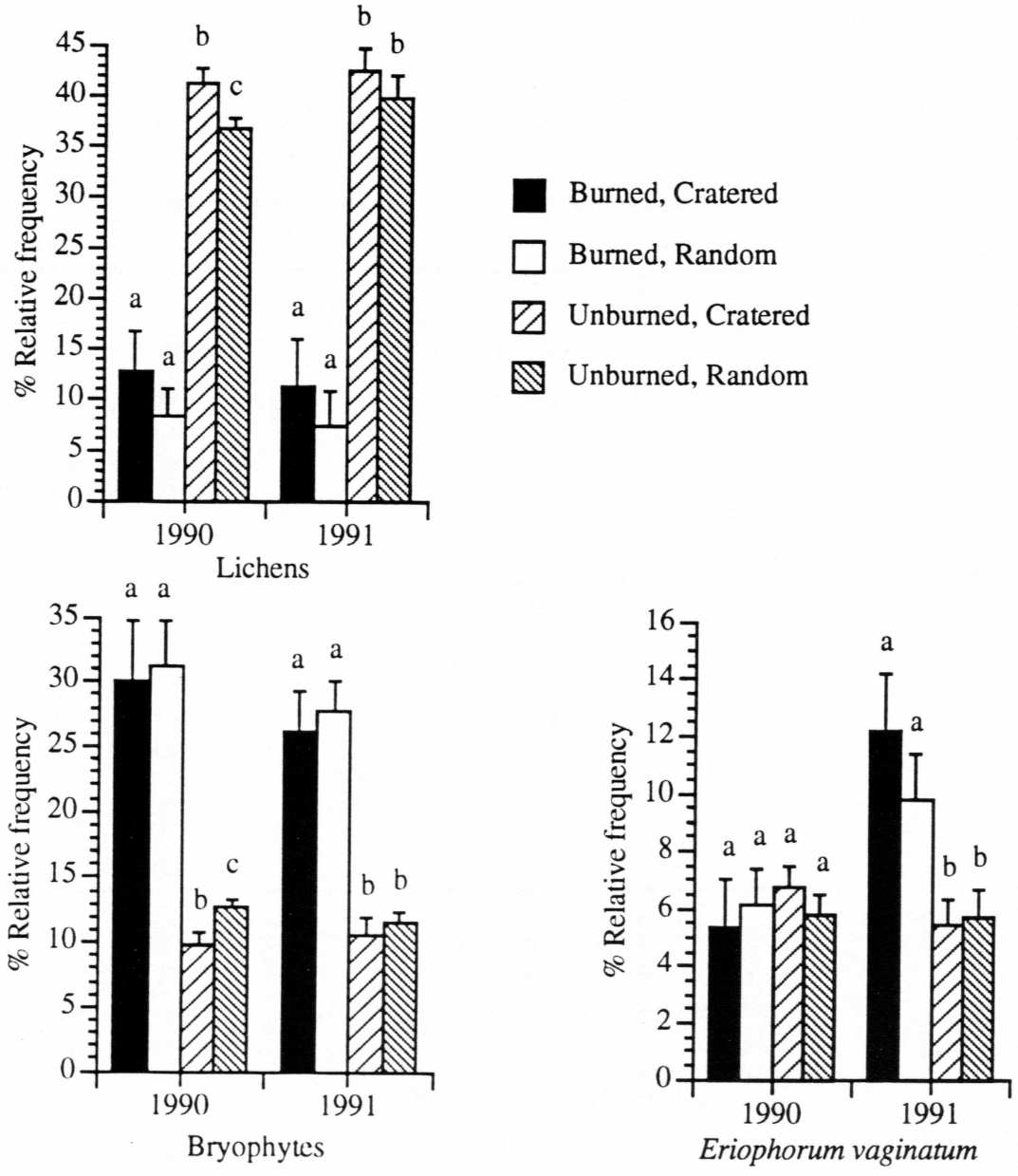

Fig. 4. Mean relative frequencies (+SE) of bryophytes, *Eriophorum vaginatum*, and lichens occurring within caribou craters at at randomly located unused points in burned and unburned habitat in northwestern Alaska, 1990 and 1991.

Different letters above bars indicate significant differences within a year. In 1990, burned plots n=19, unburned plots n=20. In 1991, burned plots n=16, unburned plots n=16.

Table 7. F-values derived from ANOVAs comparing burned and unburned plots containing caribou feeding craters and undisturbed snow in northwestern Alaska, 1990 and 1991.

Year	Variable[1]	Use [2]	F-value (Burned vs Unburned)
1990	Snow depth (cm)	C	18.03***
		R	2.54 NS
	Snow hardness (kg)	C	0.30 NS
		R	0.28 NS
	Bryophytes	C	11.59*
		R	16.11***
	Lichens	C	30.40***
		R	42.49***
	ERVA [3]	C	6.17*
		R	1.57 NS
1991	Snow depth	C	0.59 NS
		R	0.64 NS
	Snow hardness (kg)	C	0.43 NS
		R	3.45†
	Bryophytes	C	9.81*
		R	28.43***
	Lichens	C	4.87*
		R	3.27†
	ERVA	C	5.72*
		R	31.40***

[1] Vegetation variables are expressed as % relative frequency of occurrence.
[2] C=Cratered, R=Random.
[3] ERVA=*Eriophorum vaginatum*. ERVA was not selected by the stepwise procedure or entered in the MANOVA in 1990; it is included here for descriptive purposes.
* P≤0.05, ** P≤0.01, *** P≤0.001, † 0.05<P≤0.10, NS=not significant.

higher relative frequencies in unburned plots whereas bryophytes had higher relative frequencies in burned plots in both years (Fig. 4, Table 7). In 1991, *E. vaginatum* occurred at higher relative frequencies in burned plots than unburned plots, but in 1990 there was no difference in the mean relative frequency of *E. vaginatum* between burned and unburned plots.

Crater Area and Flight Transects

Caribou feeding craters were larger in unburned plots than burned plots in 1990 (P=0.0074, Mann-Whitney U-test, Fig. 5). No significant difference occurred in mean crater size between burned and unburned plots in 1991.

Data from flight transects suggested that there were more feeding craters in unburned habitat than in burned habitat in 1990 (P=0.0304, Wilcoxon test; Table 8). More feeding areas were detected in unburned habitat in 1991 as well, but sample size (n=4) was insufficient to detect statistically significant differences.

Fecal Analysis

Lichens constituted the largest portion of caribou diet (59-74%) in both years, as estimated by fecal analysis, (Fig. 6). Sedges (genera *Carex* and *Eriophorum*) increased from approximately 4% in 1990 to 12% in 1991, whereas shrubs increased to a lesser extent. Shrubs primarily belonged to the heath family. Grasses declined in 1991 and forbs (including *Equisetum* spp.) did not appear to be an important component of the winter diet in either year despite their increased availability in burned areas.

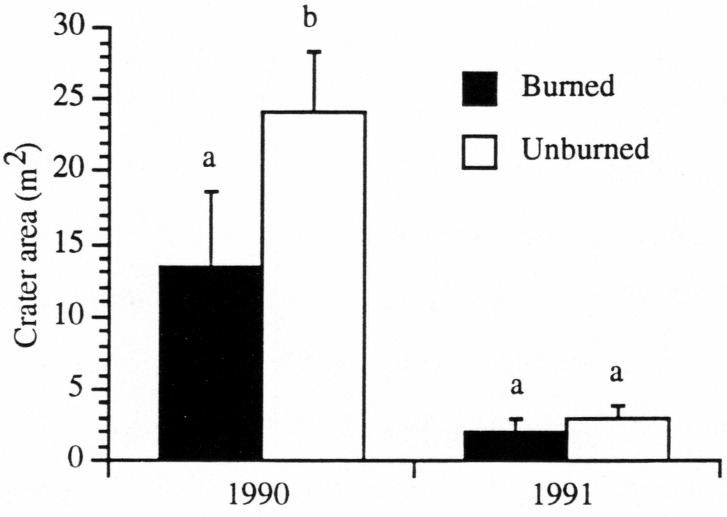

Fig. 5. Mean area (+SE) of caribou feeding craters (m^2) in burned and unburned habitat, late winter, 1990 and 1991, in northwestern Alaska.

Different letters above bars indicate significant differences within a year. In 1990, n=20 plots each in burned and unburned habitats: in 1991, n=16 plots in each habitat.

Table 8. Mean caribou feeding areas (±SE) along transects covering burned (B) and unburned (UB) habitat in northwestern Alaska, 1990 and 1991.

Year	Fire history	No. feeding areas[1] $\bar{x}$ (SE)	P-value*
1990	B	1.319 (0.573)	
	UB	8.509 (1.746)	0.0304
1991	B	4.593 (1.792)	
	UB	19.036 (9.062)	0.1939

[1] In 1990, feeding areas are reported as the mean number per linear km. In 1990, feeding areas are reported as the mean number per square km.
* P-values derived using Wilcoxon 2-sample test.

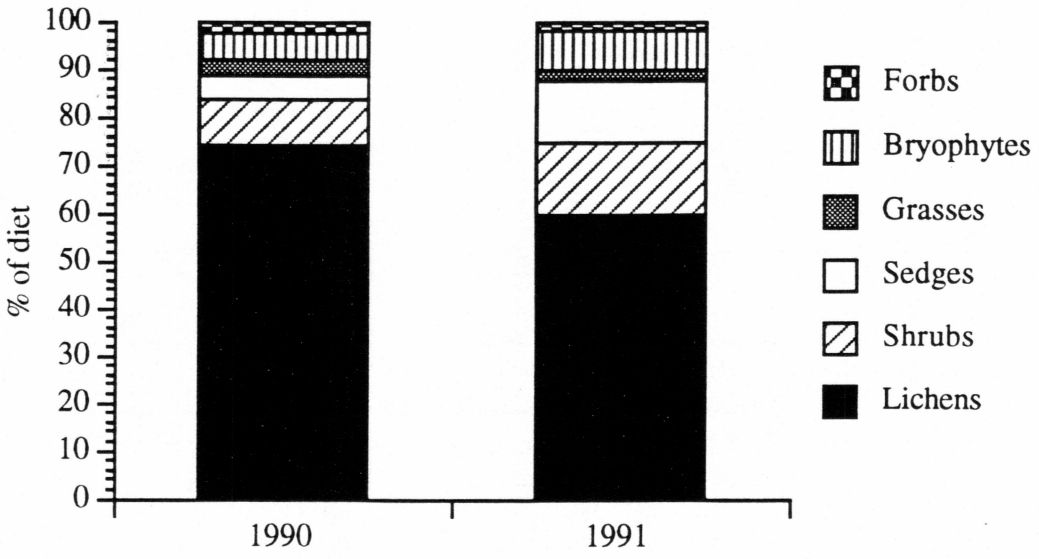

Fig. 6. Index of caribou diet composition in late winter in northwestern Alaska as determined by microhistological analysis of fecal pellets, corrected for variable digestibilities of different forage classes.

Plant Fibers, Nutrients, and Digestibilities

Lichens contained a high percentage of cell solubles in both years (Fig. 7). Charred lichens appeared to have lower levels of cell solubles and higher levels of hemicellulose and lignin than unburned lichens in 1990 (Fig. 7). Digestibility of lichens was low in both years, probably because cows were used as rumen fluid inoculum donors. Using a regression formula to calculate digestibility from NDF (Person et al. 1980), lichen digestibility was determined to be 50% in 1990 and 51% in 1991. These values are between the mean (±SD) *in vitro* dry matter digestibilities reported by Person et al. (1980) of *Cetraria cucullata* ($\bar{x}$=73.5 ±3.1), which was common on my study area, and *Cladina alpestris* ($\bar{x}$=34.4±19.5) which was less commonly encountered. The calculated digestibility of charred lichens in 1990 was 48%. Calculated values also may underestimate lichen digestibility because the regression equation was developed for use with summer vegetation and with all species and not lichens alone. Nevertheless, these calculated estimates are considerably more realistic than those obtained using cow rumen fluid.

Vaccinium vitis-idaea from unburned plots contained relatively high levels of cell solubles and lignin, had high digestibility, and had a relatively low percentage of crude protein (Figs. 7a and 8). The high percentage of crude fat (8.59%) may be attributable to the waxy leaves of this plant. There was an insufficient quantity of *V. vitis-idaea* from burned craters in 1990 to perform nutrient, digestibility and fiber analyses. There were no significant differences in fiber and nutrient composition or digestibility of *V. vitis-idaea* between burned and unburned craters in 1991 (Figs. 7b and 8b).

Eriophorum vaginatum from burned craters in 1990 contained higher levels of cell solubles than material from unburned craters (Fig. 7), but small sample size precluded statistical analysis. Levels of cellulose and hemicellulose were similar between the two samples, although the percentage of lignin was slightly larger in the unburned sample.

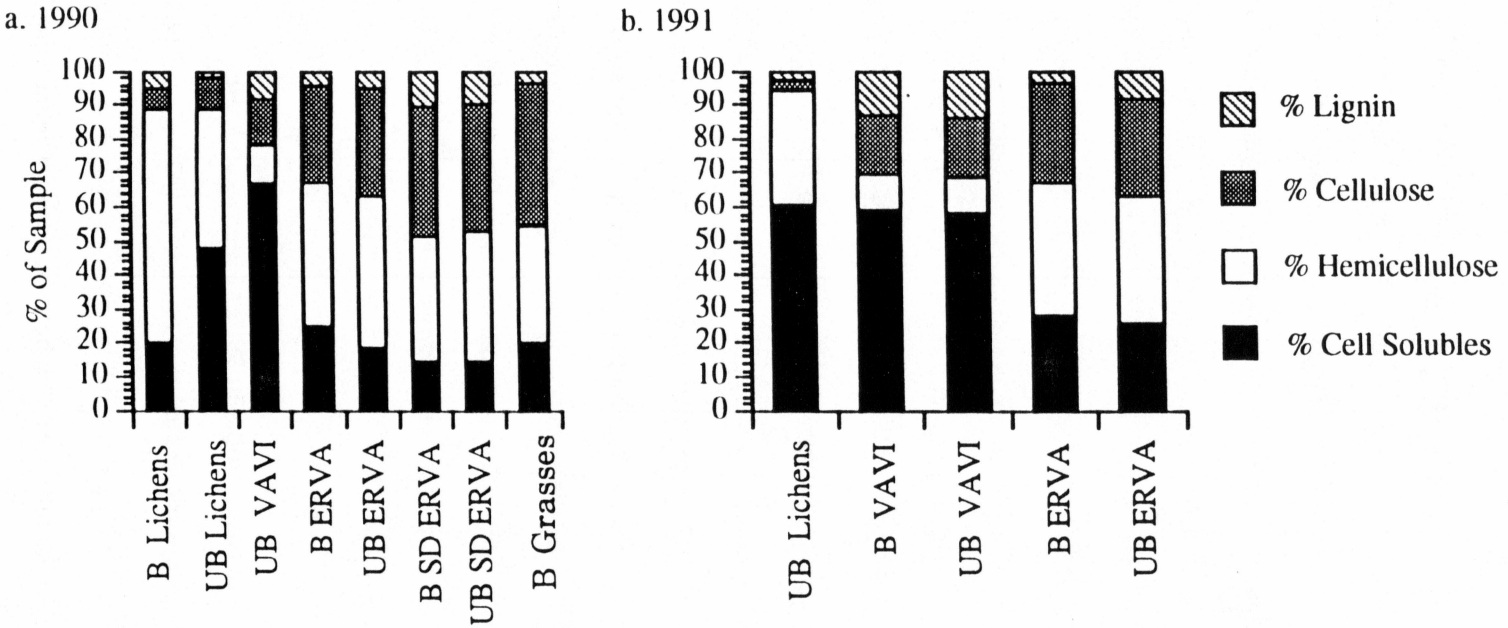

Fig. 7. Fiber composition of vegetation collected from caribou feeding craters in burned and unburned habitat during late winter in northwestern Alaska, 1990 (a) and 1991 (b). B=Burned, UB=Unburned, VAVI=*Vaccinium vitis-idaea*, and ERVA=*Eriophorum vaginatum*.

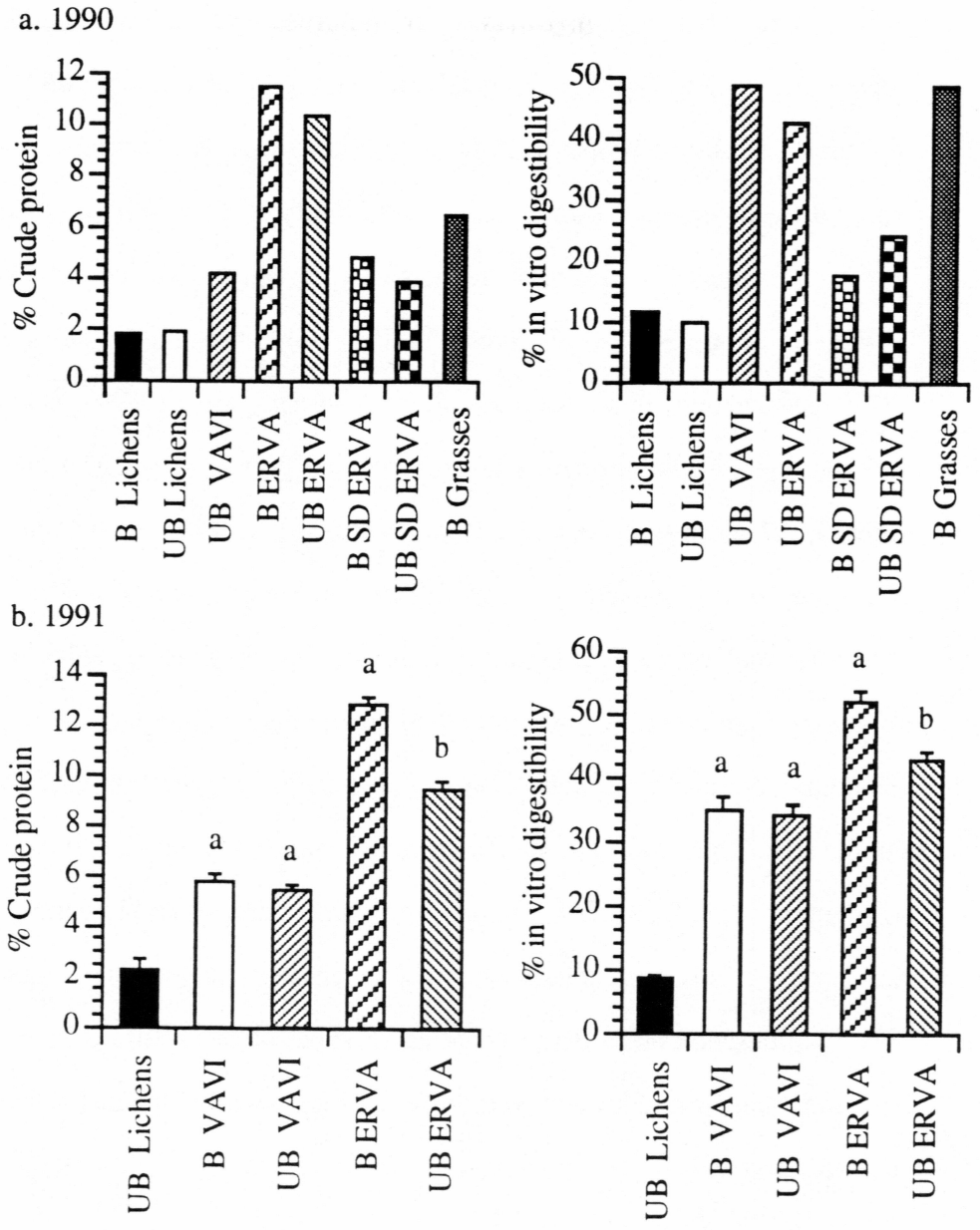

Fig. 8. Mean (+SE) percent crude protein and percent *in vitro* dry matter digestibility of vegetation collected from caribou feeding craters in burned and unburned habitat in northwestern Alaska during late winter, 1990 (a) and 1991 (b).

Different letters indicate significant differences for a species between burned and and unburned plots in 1991 ($P \leq 0.05$).

B=Burned, UB=Unburned, SD=Standing dead, VAVI=*Vaccinium vitis-idaea,* and ERVA=*Eriophorum vaginatum.*

Protein content was higher in material from burned craters, but this difference is probably not significant (Fig. 8a). Unfortunately, not enough material was collected to measure digestibility. Using Kuropat's (1984) regression equation to estimate *in vitro* digestibility from nitrogen content, I estimated the digestibility of *E. vaginatum* to be 46% and 48% from unburned and burned plots, respectively. Because 46% is close to the *in vitro* estimate of 42% for unburned *E. vaginatum* obtained using cow rumen fluid, it is likely that 48% is also a reasonable estimate for material from burned plots. In 1991, *E.vaginatum* from burned craters had significantly lower levels of lignin (P=0.03, Mann-Whitney U-test) and higher levels of protein (P=0.04, Mann-Whitney U-test, Figs. 7b and 8b). Digestibility of *E. vaginatum* was also significantly higher in burned craters (Fig. 8b).

Standing dead *E. vaginatum* had lower levels of cell solubles and protein and higher levels of cellulose and lignin than green vegetation regardless of fire history (Figs. 7a and 8a), but again, the significance of this difference was not tested because of small sample size. Digestibility of standing dead *E. vaginatum* was considerably lower than that of green material. Dead *E. vaginatum* from burned craters had lower digestibility than material from unburned craters. Grasses, which were brown in late winter and collected only from burned craters, had similar percentages of cell solubles as green *E. vaginatum.*, but hemicellulose and protein were lower and there was an increased level of cellulose (Figs. 7a and 8a).

Above-Ground Plant Biomass

Above-ground biomass of vascular plants (including *Equisetum* spp.) from the current year and total lichen biomass from random quadrats differed between burned and unburned plots (Figs. 9 and 10). Sedges, evergreen shrubs, highly preferred lichens, and nonpreferred lichens all had significantly greater biomass in unburned plots in 1990 ($P \leq 0.05$, Mann-Whitney U-test). Deciduous shrubs and moderately preferred lichens had marginally greater biomass in unburned plots ($P=0.0599$ and $P=0.0588$, respectively, Mann-Whitney U-test). Forbs and grasses had greater biomass in burned plots ($P \leq 0.05$, Mann-Whitney U-test).

Deciduous and evergreen shrubs and lichens from all categories of use had greater biomass in unburned plots in 1991 ($P \leq 0.05$, Mann-Whitney U-test). Forbs and grasses had greater biomass in burned plots ($P \leq 0.05$, Mann-Whitney U-test), and there was a trend toward greater sedge biomass in burned plots as well ($P=0.0663$, Mann-Whitney U-test) .

The biomass composition of plots differed between burned and unburned plots and between years (Fig. 11). In 1990, lichens (52.8%) and evergreen shrubs (30%) composed over 80% of the total biomass in unburned plots. Burned plots had lower total biomass, with lichens (34.6%) and evergreen shrubs (14.9%) composing < 50% of the total biomass. Forbs (including *Equisetum* spp.), which were absent in unburned plots, were an important component in burned plots. In 1991, unburned plots had lower lichen biomass than in 1990 ($P=0.0217$, Mann-Whitney U-test), and 58% of the biomass was composed of shrubs. In burned plots, sedges (mostly *Eriophorum* spp.) accounted for 50% of the biomass, a much greater percentage than in 1990 ($P=0.0011$, Mann-Whitney U-test).

The ratio of previous years' biomass (woody stems and standing dead) to current year's biomass differed between burned and unburned plots (Table 9). In 1990 and 1991, deciduous and evergreen shrubs and sedges had significantly lower ratios in burned plots ($P \leq 0.05$, Mann-Whitney U-test).

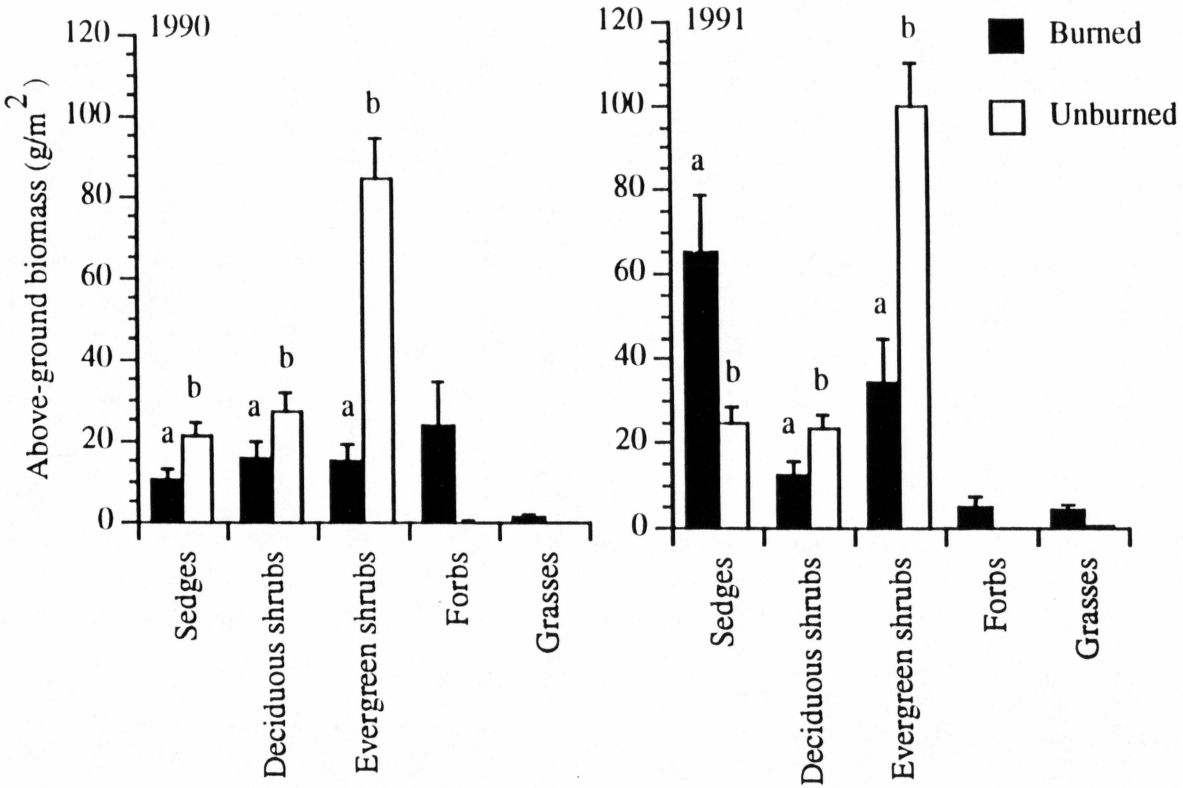

Fig. 9. Mean (+SE) above-ground summer plant biomass (current year's growth) from burned and unburned quadrats undisturbed by caribou in late winter, 1990 and 1991, in northwestern Alaska.

Different letters indicate significant differences in a plant category between burned and unburned plots within each year ($P \leq 0.05$, Mann-Whitney U-test).

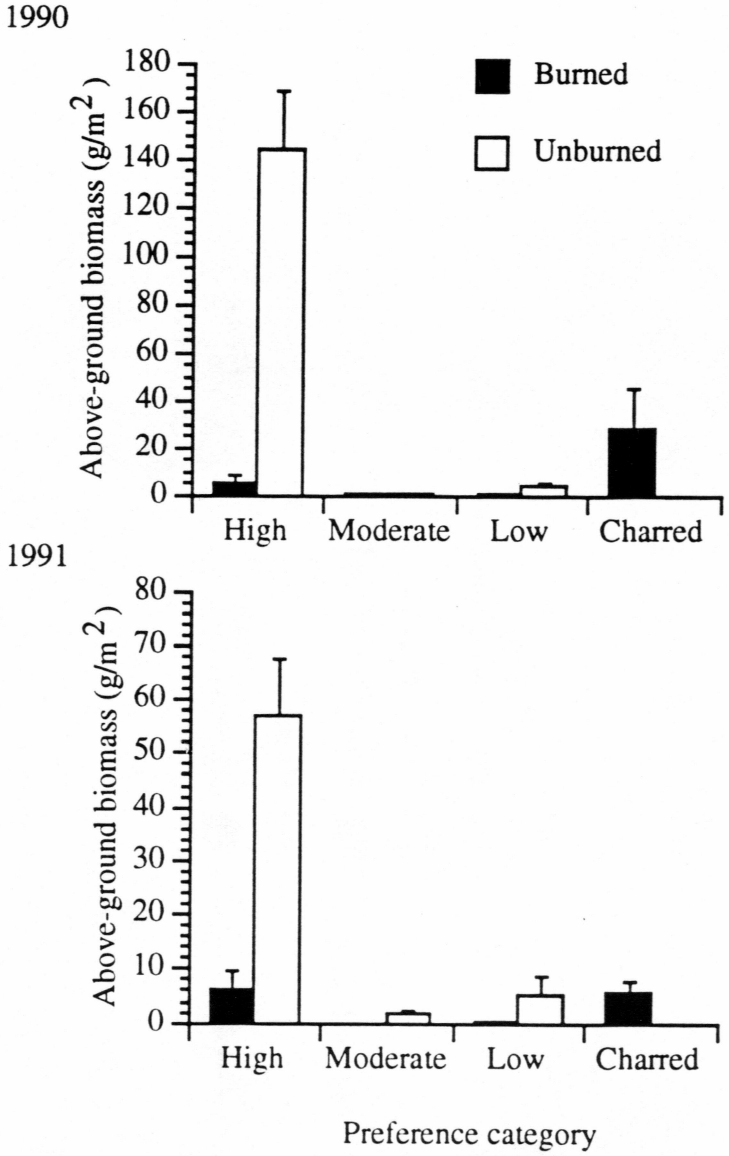

Fig. 10. Above-ground biomass ($\bar{x}$+SE) of lichens collected in summer from burned and unburned quadrats undisturbed by caribou in late winter in northwestern Alaska, 1990 and 1991.

Preference categories are as follows:
High=*Cetraria* and branching *Cladina* spp.
Moderate=*Peltigera, Parmelia, Alectoria,* and *Stereocaulon* spp.
Low=Cuplike *Cladonia* spp.

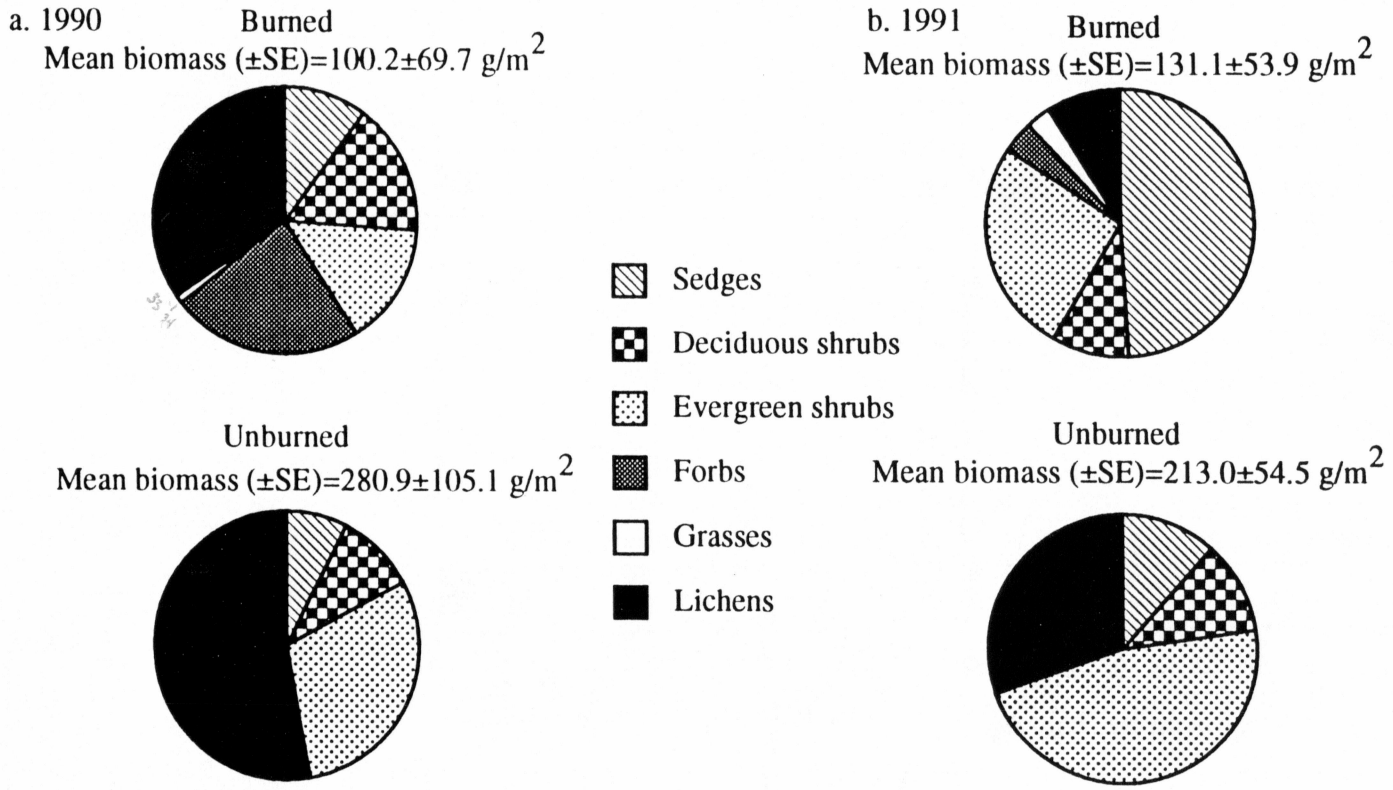

Fig 11. Composition of above ground biomass (excluding previous years' stems and litter) from burned and unburned plots in northwestern Alaska, 1990 (a) and 1991 (b).

Table 9. Mean ratios (±SE) of previous years' to current year's above-ground summer plant biomass from quadrats undisturbed by caribou in late winter in northwestern Alaska, 1990 and 1991.

Year	Plant group	Fire history[1]	Previous:current (g/m^2) $\bar{x}$(SE)[2]
1990 (n=19 burned, n=20 unburned)	Sedges	B	0.233 (0.123)***
		UB	1.002 (0.165)
	Evergreen shrubs	B	0.209 (0.038)***
		UB	0.503 (0.029)
	Deciduous shrubs	B	0.303 (0.126)**
		UB	1.285 (0.370)
1991 (n=16 burned, n=16 unburned)	Sedges	B	0.669 (0.085)***
		UB	1.585 (0.183)
	Evergreen shrubs	B	0.773 (0.156)**
		UB	1.212 (0.129)
	Deciduous shrubs	B	1.321 (0.713)*
		UB	1.852 (0.300)

[1] B=Burned, UB=Unburned.

[2] Independence of plant groups is assumed.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$ between burned and unburned plots for each plant group, Mann-Whitney U-test.

DISCUSSION

Snow Characteristics

Snow depth and hardness were the most influential determinants of crater location by caribou. Caribou consistently cratered in softer, shallower snow than was present in adjacent unused areas in both years (Fig. 3). Thus, the prediction that caribou differentially select feeding sites on the basis of snow conditions was supported by the results. Mean depths at crater edges (29-44 cm) were below reported upper limits (LaPerriere and Lent 1977, Brooks and Collins 1984, Russell and Martell 1984, Adamczewski et al. 1988), but mean depths in unused areas were near 50 cm and depths at individual random points occasionally exceeded 1 m. Hardness values exceeded 17,000 g, and cratering ability by caribou may have been impaired. Henshaw (1968) suggested that the hardness threshold in northwestern Alaska, above which cratering by caribou was impeded, was 6,500 g/m^2. Hard snow, however, may facilitate travel (LaPerriere and Lent 1977) and therefore reduce energy expenditure during migration.

The prediction that fire affects snow conditions was not supported, although in 1991 snow at undisturbed points was marginally harder in burned than unburned plots ($P=0.0731$). Reduction of shrubs in the burn may have increased settling and compaction of snow, thereby increasing hardness. Mean depth at undisturbed points did not vary with fire history although snow at crater edges was shallower in burned plots in 1990. Rather than an effect of fire, this is a result of caribou digging in shallower snow in burned plots. Schaefer and Pruitt (1991) reported increased snow depth after burning in the taiga, probably due to the absence of snow interception by crowns of standing trees. Brooks and Collins (1984) reported that snow depth on the Seward Peninsula, Alaska, was linearly related to the height of tundra vegetation, leading to the assumption that removal of vegetation by fire would, if anything, reduce snow accumulation. Vegetation may only

grow where it can be protected by deep snow, however, and removal of vegetation by burning may not affect snow depth. Contrary to conditions on burned taiga range, travel on burned tundra by caribou is facilitated by the absence of fallen trees, which tend to intercept and prevent settling of snow. Fire may affect snow cover in other ways, such as enabling earlier snow melt.

Selection of soft, shallow snow for cratering ostensibly reduces the energetic costs of foraging caribou and reindeer in winter (Fancy and White 1985), but this behavior is not energetically advantageous if forage availability in craters is insufficient to justify the cratering effort. Mean crater size may serve as an indication of cratering effort (i.e. energy expenditure), although this index may also reflect patch size of the forage or number of caribou using the crater. Mean crater size was significantly smaller in burned plots in 1990, suggesting that harder snow or low forage availability reduced cratering effort. This is supported by the observation that despite similar depths between burned and unburned random points, caribou consistently cratered in shallower snow in burned plots, presumably to minimize effort digging through deeper snow. Perhaps caribou were unable to smell the low quantities of forage, particularly the reduced quantity of lichens, in burned plots under deeper snow (Helle 1984). Most burned plots in 1990 contained sparse vegetation consisting primarily of post-disturbance bryophytes, forbs, and grasses with few lichens. Potential difficulties in detecting forage in the burn coupled with the high occurrence of nonforage species may have resulted in caribou exerting limited effort in digging craters.

Mean crater size was the same between burned and unburned plots in 1991, possibly because of an increased availability of winter-green forage in the burn in 1991. Craters in the burn in 1991 were primarily located in areas containing resprouting tussocks, and the high availability of winter-green forage may have stimulated caribou to expend as much energy digging in burned plots as unburned plots. In addition, 4 of the 16 burned

plots contained unburned islands with craters that approached sizes similar to those occurring in unburned plots. Crater size was significantly smaller in 1991 than 1990, however. Poorer forage availability, harder snow, or increased disturbance interrupting cratering activity are potential explanations for the smaller craters in 1991. Skogland (1978) reported that reindeer dug shallower craters in harder snow, and crater area may have been similarly affected by the harder snow in 1991. Collins and Smith (1991), however, reported that the mean bottom area of craters was not related to depth or hardness but was weakly correlated with total cratering time. Helle and Tarvainen (1984) noted that length of the digging period was positively associated with the amount of forage lichens, and the low biomass of preferred lichens in 1991 could have resulted in short digging periods and, consequentially, small crater size. Caribou arrived in my study area three weeks later in 1991 than 1990. Pressure to reach their calving grounds may have led caribou to more quickly traverse the study area in 1991, spending little time feeding in an area.

Plant Relative Frequency and Biomass

Lichens were the major component of the caribou diet in both years. Previous estimates of the percentage of winter diets are similar to my results (60%, Scotter 1971; 63%, Adams and Connery 1983; 70-76%, Hinkes and Campbell 1984). Caribou preferentially cratered for high relative frequencies of lichens and avoided high frequencies of bryophytes in 'normal' unburned plots in 1990. This supports the prediction that cratered and unused areas contain different types and amounts of vegetation. Helle (1984) observed that 'sniffing sites,' where reindeer attempted to smell forage but did not dig, contained 3 times the amount of moss biomass than adjacent craters, supporting my observation that bryophytes occur in craters in similar proportions to their availability or are avoided. Mean relative frequencies of vegetation variables did not differ between cratered and random quadrats in burned plots in 1990 or between cratered and random quadrats in

burned and unburned plots in 1991. Crater sites in these instances were correlated with snow characteristics alone. Although lichens are important in the winter diet, the significance of snow depth and hardness is not surprising; other researchers have claimed that selection of crater locations is based primarily on snow conditions and only secondarily on vegetation types beneath the snow (White et al. 1981, Miller et al. 1982).

Uniform distribution of vegetation within plots may be partly responsible for the absence of selection for particular forage species in burned plots in 1990 and in both types of plots in 1991. Vegetative composition looked relatively homogeneous within my plots, but larger plots may have extended into different habitats containing less desirable forage species. If vegetation within plots was relatively homogeneous, caribou could have foraged in previously unused portions of my plots as snow conditions became more favorable. With the exception of unburned islands, plots were especially uniform in burned areas, consisting primarily of post-disturbance species, resprouting tussocks, and burned organic matter.

Plant relative frequencies and above-ground biomass differed between burned and unburned plots (Figs. 5, 13, and 14), supporting the prediction that burning affects vegetation composition and quantity. Vegetation in burned plots was similar to that described by Racine (1981) after extensive fires on the Seward Peninsula in 1977. Burned plots in 1990 contained lower relative frequencies of lichens and higher relative frequencies of bryophytes than unburned plots, which is the converse of conditions caribou favored in unburned plots. Relative frequency of lichens remained lower in burned plots in 1991, but relative frequency of *E. vaginatum* in burned plots exceeded that in unburned plots. This is due to both the ability of tussocks to quickly resprout after burning (Hall et al. 1978, Racine 1979) and an apparent increase in number of *Eriophorum* seedlings. This apparent increase in seedling number is attributed to increased flowering and fruiting (Wein and

Bliss 1973), and caribou of the Western Arctic Herd have been known to eat *Eriophorum* flower heads in late May and early June (Davis and Valkenburg 1978).

Forbs were not as common in burned plots in 1991 as they were in 1990. Many burned plots in 1990 had a higher shrub component prior to burning than in 1991 when most craters, and therefore most plots, in the burn were located in areas where tussocks were dominant. Shrubby areas tended to be burned down to mineral soil during the 1977 tundra fires on the Seward Peninsula, providing suitable habitat for invading forbs and grasses (Racine 1979). In tussock tundra in my study area, however, shrubs growing on tussocks were often protected from the fire and were an important component of the post-fire plant community. Racine (1981) noted that burned tussock tundra was revegetated mainly by sprouting of pre-fire species, whereas areas dominated by dwarf birch and ericaceous shrubs were more severely burned and were colonized by graminoid seedlings, forbs, and bryophytes.

Plant relative frequencies provide information regarding the relative importance of a species in a plot while biomass measurements estimate quantities of vegetation present. Generally, biomass trends paralleled relative frequency results in this study. The annual biomass of sedges, deciduous and evergreen shrubs, and the total biomass of highly and not preferred lichens was greater in unburned plots in 1990, but by 1991 sedges had greater biomass in burned plots. This corresponds to the increase in the mean relative frequency of *E. vaginatum* in burned plots that resulted from vigorous resprouting and increased seedling establishment. Because craters in burned plots were usually centered on resprouting tussocks, whereas random quadrats often were centered on inter-tussock spaces or dead tussock stumps where most vegetation had been destroyed, mean biomass

of *E. vaginatum* in burned plots would have been even greater if craters were clipped rather than, or in addition to, random quadrats. Inter-tussock spaces in unburned plots, in contrast, often contained lichens.

A low ratio of previous years' to current year's growth, as occurred with *Eriophorum vaginatum* in this study, enables herbivores to obtain more green material with each mouthful of forage (Hobbs et al. 1991). A ratio > 1 indicates greater quantities of woody or standing dead material than nutritious green vegetation. Burned areas had significantly lower ratios than unburned areas, thereby increasing the foraging efficiency of caribou feeding on winter-green vegetation in burned plots.

Mean lichen biomass was severely reduced by burning in both years, with the exception of moderately preferred genera in 1990. There was approximately a 25-fold difference in biomass of highly preferred lichen species between unburned and burned plots in 1990, supporting previous claims that fire devastates lichen ranges, at least in the short term. This loss of biomass can be misleading, however, because many of the destroyed lichens may have been over-mature, composed largely of dead podetia bases that are not used by caribou. *Cladina* lichens undergo three stages of development: 1) growth accumulation (averaging 10 years) when there is a constant increase in podetium size and annual growth, 2) growth renewal, when the podetium begins to die at the base but new growth continues at the maximum rate attained during the first stage, and 3) podetium degeneration, when lower portions of the podetium die at rates equal to or greater than the accumulation of new growth (Andreev 1954). Although the growth renewal phase may be long, considerable portions of a 100-year-old lichen stand will be in the podetium degeneration stage (Andreev 1954). Indeed, when the lichen *Cladina mitis*, which was common on my study area, is fully grown, it adds new tissues at the same rate that older tissues are lost through decomposition (Gaare 1986). Miller (1976, 1980) reported that even though the largest standing crops of lichens in northcentral Canada occurred in 57-107

year-old stands, caribou were attracted to lichens in 40 year-old stands, and increased age was not necessarily correlated with greater biomass of lichens.

This is likely to occur because of the higher percentage of living material in younger stands, and is contrary to claims that old-growth lichen stands are preferred caribou habitat. It has even been suggested that Swedish lichen ranges with light use by reindeer be scorched to maintain high productivity (Skuncke 1969).

Despite similar values of relative frequency of lichens in random quadrats of unburned plots in both years, the total biomass of lichens in unburned plots was significantly lower in 1991 than 1990 (Figs. 10 and 11). This may reflect an overall decline in range quality or inaccessibility of better lichen ranges due to harder snow during the winter of 1991. If range quality is indeed declining, the rate of decline due to grazing was likely accelerated by reduction in overall abundance of lichens by fire. Using the radiocesium method for determining lichen intake, it was estimated that an 80 kg animal ate approximately 5 kg lichen/day (Holleman et al. 1979). When this figure is considered along with the number of animals potentially using this winter range and the amount of range actually accessible to caribou in winter, the observed decline in lichen biomass between years may have consequences for herd health if the trend continues.

Under some circumstances, however, lichens may not be crucial for the survival of *Rangifer* populations over winter. In situations where lichens are neither widely available nor a major component of winter diet (Skoog 1968, Kishchinskii 1971, Parker 1978, Leader-Williams 1980, Leader-Williams et al. 1987) fires may not be as devastating as previously reported (Bergerud 1974b). In other instances, lichens may be used only in proportion to their availability (Miller 1980, White and Trudell 1980, White et al. 1981). Most instances where caribou survive with low lichen abundance, however, occur in the High Arctic (Klein 1982), where caribou densities are low, or on islands with strong maritime influences. In these situations, abundant forage, low levels of insect harassment

and predation, and absence of migration allow caribou and reindeer to feed efficiently in summer and accumulate large fat reserves to compensate for low-quality forage in winter (Reimers 1977, Klein 1982, Gates et al. 1986). On oceanic islands (Kishchinskii 1971, Parker 1978, Thomas and Broughton 1978, Reimers 1980), moderate winter conditions may allow caribou and reindeer to survive with limited dependence on lichens (Klein 1982). In any case, sufficient vascular-plant forage of high quality must be available for their survival. Furthermore, the proportion of lichens in the diet increases as winter progresses (Miller 1974, Andreev 1975, Klein 1982), and studies reporting low use of lichens in early winter may not be representative of dietary habits in mid- and late winter (Klein 1982).

Forage Quality

The prediction that burning indirectly influenced crater site selection by affecting forage quality, was partially supported by these data. Unburned lichens had a high percentage of cell contents, making them rich in readily usable energy (Person et al. 1980), but burning reduced the percentage of cell solubles, lowered predicted digestibility, and increased proportions of hemicellulose and lignin. Nevertheless, it appeared that caribou detected and cratered for charred lichens in 1990. These lichens, often in the form of small fragments that may have been difficult to eat, rarely occurred in burned plots in 1991.

Vaccinium vitis-idaea had a relatively high ratio of lignin:cellulose, which is associated with low digestibility. Palatability may also be inhibited by the waxy leaves and the presence of secondary compounds (Person et al. 1980). There was insufficient material from burned plots for tests in 1990, but material from 1991 did not differ in fiber composition between burned and unburned plots. Likewise, there were no differences in digestibility or crude protein content as a function of fire history.

Burning resulted in lowered lignin levels in *Eriophorum vaginatum*, and crude protein and digestibility were higher in burned plots. This protein rich, easily digestible material may ease physiological stress in caribou, particularly pregnant females, that have been subsisting on lichen diets low in protein (Jacobsen et al. 1981, Rognmo et al. 1983). Often these nutritionally stressed animals do not encounter newly emerged green forage until after reaching their calving grounds (Duquette and Klein 1986). Green *Eriophorum* shoots and floral buds were commonly visible emerging through shallow snow, especially in burned areas and on low ridges with earlier snow melt. White et al. (1981) suggested that with supplementation by high protein winter-green material, a lichen-dominated winter diet could be as nutritious as summer diets. Robinson and Spindler (1989) observed that caribou distribution was similar inside and outside of the burn perimeter, but the density of animals was doubled at the edge. Caribou may have congregated at edges because these areas provide easy access both to lichen stands and nutrient rich green material. Caribou within the burn also have some access to lichens surviving in unburned islands. Hinkes and Campbell (1984) noted that caribou extensively used recent burns at Farewell, Alaska. Use was centered around unburned islands and adjacent unburned habitat, but caribou freely moved in and out of the burn.

The duration of changes in nutrient balance and productivity of vascular plants following fire is unknown. As succession progresses, litter accumulates and nutrients are tied up while bryophyte and lichen productivity increases, the ground becomes insulated by vegetation, and soil temperatures drop (Viereck and Schandelmeier 1980, Brown 1983). Crude protein and digestibility of *E. vaginatum* were still enhanced 2 and 3 winters after burning in this study, but it is not known how much longer this situation will persist. *E. vaginatum* displayed heightened productivity of flower heads for 3 to 6 years following the 1977 fires on the Seward Peninsula, but by 10 years there was no difference in production of flower heads between plants in burned and unburned habitat (Racine et al. 1987). Thaw

and active layer depths also increased by 30-50% following these fires, but after 5 to 6 years they had returned to pre-fire levels (Racine et al. 1987). Increase in relative frequency of *E. vaginatum* in burned plots is likely a combination of these factors: heightened nutrient availability in the ash layer and expanded active layer, increased seed production, and increased temperature near meristems stimulating production of daughter tillers (Fetcher 1985).

High levels of lignin and low protein content in standing dead *E. vaginatum* stems further supports the notion that caribou benefit from decreased biomass of standing dead material in the burn. If *E. vaginatum* from burned plots exhibited enhanced digestibility in 1990 as it did in 1991, this benefit was apparently lost as vegetation senesced. Senesced sedges and grasses generally have low nutrient content and are poorly digested by herbivores (White et al. 1975, Person et al. 1980), and Holt (1980) observed that caribou in west Greenland avoided areas with large quantities of standing dead biomass in summer. Grasses common in burned areas, primarily *Calamagrostis canadensis*, were brown in late winter and had high levels of cellulose. Their low abundance in fecal pellets suggests that they were not used, despite their relatively high digestibility.

Effects of Burning on Diet Selection

Diet composition did not differ depending on fire history was not supported. Despite differences in mean relative frequency, mean above ground biomass, and vegetation quality between burned and unburned plots, winter diets of caribou did not differ inside and outside of the burn perimeter. The burn by use interaction in the MANOVA was not significant, indicating that there were no overall differences in selection of crater sites in relation to fire history. Caribou did not change their foraging pattern and select post-fire species such as fireweed when in burned areas. They continued to crater where snow conditions were favorable and, if unburned plots in 1990 were examples of

'normal' cratering activity, where there were high frequencies of lichens and low frequencies of bryophytes. Although fecal pellets from burned and unburned plots were combined prior to analysis, the proportions of forbs and grasses in the diet were minimal. The only support for this prediction is the increased relative frequency of *E. vaginatum* in burned craters and the corresponding increase of this species in fecal pellets in 1991. Hinkes and Campbell (1984) also noted that caribou ate more *Eriophorum* in burned areas than at unburned sites. This may be a consequence of increased availability of *Eriophorum* rather than choice because most of the diet was composed of lichens in 1991, and evidence suggests that caribou still search for lichens in burned areas. Schaefer and Pruitt (1991) reported that dietary composition of woodland caribou (*Rangifer tarandus caribou*) in burned areas was similar to the pre-fire diet. These woodland caribou intensively used remaining lichens, reinforcing the concept that lichens were the preferred forage item.

Although diets did not differ between burned and unburned habitat, flight transects in 1990 indicated that caribou preferred to forage in unburned habitat, where lichens were plentiful, and transects in 1991 suggested a similar trend. Burned areas were frequently employed as travel routes, but cratering activity adjacent to these trails was much less common than was observed along trails in unburned habitat. A similar discrepancy between number of craters near trails in burned versus unburned habitat was observed by Miller (1980). Despite the concentration of caribou at the burn boundaries soon after the fire (Robinson and Spindler 1989), caribou appeared to forage more in unburned habitat in 1990 and 1991. Transect data are somewhat difficult to interpret, however, because caribou were not present in large numbers in some unburned habitat outside of the immediate study site during my winter field seasons. Because snow and vegetation sampling were not conducted outside of the study area, it is not known whether these areas were unused because of unfavorable conditions or because of other factors such as historical migratory

patterns, proximity to escape terrain, chance, or other environmental components (Bergerud 1974c, White et al. 1981) that may be important on a landscape scale.

Fire clearly had a major effect on forage availability in this study, but it did not affect selection. It is important, however, to distinguish between the long and short term effects of fire (Klein 1982, Schaefer and Pruitt 1991). The long-term influences of fire are important on a landscape level, and more research is needed on the interaction of fire, vegetation, and herbivory in northern ecosystems. Fire enhanced nutrient status, flowerhead production, and productivity of *Eriophorum vaginatum*, and removed unpalatable dead material, making burned tussock-tundra an attractive feeding site for caribou in late winter and possibly for other herbivores in different seasons. This combination of increased grazing and nutrient availability may have stimulated compensatory growth of *E. vaginatum* and created a positive feedback mechanism where increased productivity and enriched nutrient status can be maintained for a longer period than if fire was acting independently. *E. vaginatum* can tolerate moderate levels of grazing, and new growth following defoliation had higher levels of nitrogen, phosphorus, and potassium than the original vegetation (Chapin 1980). McNaughton (1984) proposed that aggregations of grazing animals can modify vegetation to enhance its value to the grazer, but Lent and Klein (1988) deny that migratory herds of caribou would affect vegetation in this manner because large aggregations remain in one area for too short a period for grazing to stimulate growth. The flush of nutritious vascular vegetation following fire may induce males and nonpregnant females to remain in burned areas longer than usual before continuing their northward migration, thereby increasing grazing pressure on post-fire vegetation and allowing compensatory mechanisms to occur. Hobbs et al. (1991) noted that grassland nutrient cycles may be regulated by grazing and fire in different ways than if each process occurred alone. Evidence supporting coevolution of tundra plants and animals may

be weak (Lent and Klein 1988), but fire has not been included as a factor in this relationship before.

MANAGEMENT IMPLICATIONS

Fire management tends to be a controversial subject because of the many issues involved. Only recently have managers, accepting that fire is a natural and often necessary process, allowed some fires to burn without extensive control efforts. This practice is not without problems, however. As more people move into the countryside, building year-round homes or vacation retreats, it will become increasingly common that fires are extinguished in defense of human life or property. Controversy over management practices was heightened during the 1988 fires in Yellowstone National Park (Christensen et al. 1989, Elfring 1989) when many people believed that allowing fires to burn would diminish recreational and scenic beauty of the area, regardless of claims that wildlife productivity and viewing opportunities would likely be enhanced in the future. As numbers of natural, wild places decrease, it is understandable that people are increasingly unwilling to forego short term losses of the remaining habitat to fire. There are also economic, as well as aesthetic, concerns involved in fire management. The timber industry usually does not have access to logging in burned sections of federally designated wilderness areas or National Parks, and the industry views standing dead, charred trees as lost economic opportunities. Wildfires also provide income for thousands of people annually, including fire-fighters, administrative staff, and private agencies involved in catering to fire-fighters' needs.

Fire management in Alaska includes other issues in addition to the ones already mentioned. The Alaskan taiga has evolved with short intervals between naturally occurring large fires (Viereck and Schandelmeier 1980) and many plants and animals have evolved to take advantage of different successional stages following fire. Although many fires in Alaska, both on tundra and taiga, occur in areas of low human population, they may threaten villages, Native allotments (ANCSA, US Public Law 92-203), and subsistence lifestyles. Fire-fighting can provide a much needed source of income to inhabitants of

remote villages, but fires occurring in these remote areas are often expensive to control. It may not be cost effective to fight a fire that likely will be extinguished by rain or snow rather than human effort. Managers must take these issues into account in addition to biological concerns.

The Waring Mountains Fire started in a portion of the Selawik National Wildlife Refuge that was designated for limited fire suppression (Jerry et al. 1988). The decision to extinguish the fire was made to protect Native allotments and caribou migratory habitat. Local residents were concerned that burned areas would deflect migrating caribou and negatively affect their subsistence lifestyle. The fire also generated thick smoke that hindered air travel, which is the primary source of transport during medical emergencies, and caused or worsened respiratory problems (M.G. Sheldon, pers. comm.). The fire cost over $4,000,000 to fight, and allotments and habitat were nevertheless destroyed (Jerry et al. 1988).

Safety and health problems often overshadow and limit biological concerns that managers may have, but I believe that there are still ways to help minimize detrimental effects of fire on wildlife. First, it is essential that managers understand the distinction between long-term and short-term effects of fire. They must recognize that some enhancements to wildlife habitat resulting from fire, such as nutrient enrichment, are strictly short-term benefits that may only persist for a few years following fire. Nonetheless, these short-term mosaics of favorable forage shift across the landscape with time as succession proceeds on old burned sites, and new fires are ignited. Thus, taken collectively on a large spatial scale, short-term effects are important to wildlife because they result in different habitats, with different values for wildlife, existing in varying proximity to each other. Users of managed lands may not appreciate the importance of long-term effects of fire, such as the maintenance of habitat diversity. It is important to educate the public about these long-term benefits so that they fully realize the role of fire in the environment, despite

potential emigration of some wildlife species from burned areas. Managers in Alaska have the additional concern that although fire may be a positive influence in the long run, it may reduce the amount of wildlife available for subsistence hunting in the short term.

If fire suppression is deemed necessary to maintain short-term continuity of human use, wildlife, or other resources, it would be helpful to note areas of special importance to wildlife where suppression would be cost- and time-effective. Parts of the Waring Mountain burn were in sandy areas rich in lichens and contained numerous and well worn caribou trails. In one instance, I observed a caribou trail that acted as a natural fire-break. It would be easy to construct a fire-line in such an area, and valuable habitat may have been preserved. This is contrary to the situation occurring in tussock tundra, where thick vegetation and organic matter make it difficult to control the spread of fire. In addition, fire ensures the existence of tussock tundra by removing vegetation that may stifle tussocks, and caribou may derive short-term benefits from enhanced nutrient and productivity levels in *Eriophorum vaginatum*.

Reindeer herders with limited rangeland available to them may be particularly concerned about fire on winter range. Lichens will be in short supply for decades after the short-term benefits of fire are no longer realized. Periodic scorching of previously burned sites to maintain high productivity and enhanced nutrient status of winter-green vegetation is a possibility that warrants further examination. Plant species able to resist fire, such as *E. vaginatum*, are more likely to survive burning if they are in the adult stage (Rowe 1983). Experimentation would be necessary to determine the fire rotation period that ensures survival and maximum productivity of forage species.

In this study, I observed that biomass of lichens in unburned plots was much lower in 1991 than in 1990. Because locations of plots were dependent on crater site, my data can not be considered a general survey of range condition, and this reduction in biomass may be a result of caribou behavior rather than a sign of range deterioration. The relative

frequency of lichens was similar between the two years, however, and considering the large size of the Western Arctic Caribou Herd, I believe that there is sufficient cause for a more thorough study on the status of lichens in my study area and perhaps in wintering areas to the south.

Additional research on long-term effects of fire on the tundra is clearly necessary. The questions of local residents concerning fire and subsistence use must be addressed, and more research is needed to properly answer these questions. In addition, effects of fire on other species of tundra wildlife, such as waterfowl and furbearers, and their habitat must be studied. Only after we have more complete data on long-term consequences of fire can managers weigh costs and benefits of fire on wildlife along with costs and benefits of suppression.

CONCLUSIONS

Caribou fed in shallower, softer snow than occurred in adjacent undisturbed areas. Snow at undisturbed areas often exceeded the 50-70 cm limit above which cratering activity is impaired. Fire did not affect snow depth, although caribou craters were found in shallower snow in burned plots than in unburned plots despite similar depths in unused areas. Snow was marginally harder at burned random points than at unburned random points in 1991, possibly because likelihood of compaction increased after vegetation was removed by fire.

Although snow characteristics, particularly depth, were major determinants of crater location, forage availability played a role. Caribou cratered where there were high relative frequencies of lichens and low relative frequencies of bryophytes in unburned plots in 1990. No differences were detected between cratered and random quadrats in burned plots in 1990 or in any plots in 1991. Despite this absence of differentiation, lichens were a major component of winter diet in both years.

Burning resulted in an increase in relative frequency of bryophytes and a decrease in frequency of lichens. This is contrary to conditions favored by caribou in unburned plots in 1990. Post-disturbance species such as *Epilobium angustifolium*, *Senecio congesta*, and *Calamagrostis canadensis* were common in burned plots but virtually nonexistent in unburned plots. In 1991, relative frequency of *Eriophorum vaginatum* in burned plots exceeded that in unburned plots. *E. vaginatum* vigorously resprouted after burning and was often the dominant plant species in burned plots. The importance of winter-green sedges as a dietary supplement for caribou in winter has been documented in the literature.

Lichen biomass was severely depleted by burning, and biomass of evergreen and deciduous shrubs was also low in burned plots in both years. Some dwarf shrubs growing on the tops of tussocks were protected and may act as sources for vegetative reproduction.

Lichens were present in unburned islands, and fragments of these are potentially important for the regeneration of lichens in the burn. There were no signs of lichen regeneration in the burn at the time of this study. *E. vaginatum* biomass was lower in burned plots in 1990, but by 1991 its biomass was greater in burned plots than in unburned plots. This is attributed to its ability to resprout and seed in following fire.

Craters were larger in unburned plots than in burned plots in 1990, indicating that caribou expended more energy foraging in unburned areas. It is likely that caribou were unable to detect reduced quantities of forage, especially lichens, in the burn and were unwilling to exert energy in digging. There was no difference in crater area between burned and unburned plots in 1991. Craters in 1991 were often located on resprouting tussocks or unburned islands that had some forage value, while many craters in 1990 were located in areas largely vegetated with post-disturbance species. Greater availability of green forage in the burn in 1991 may have caused caribou to exert more energy in cratering, and crater area was more similar to that found in unburned plots. Mean crater area in both burned and unburned plots was smaller in 1991 than in 1990, however. There are a number of possible explanations for this. Snow was considerably harder in 1991 than in 1990, possibly hindering cratering and resulting in smaller craters. Lichen biomass in unburned plots was lower in 1991, which may indicate a deterioration in range condition or unavailability of superior lichen ranges due to more severe snow conditions, and it may not have been efficient to dig large craters to reach tussocks. Many craters in 1991 were just large enough to reach the green vegetation on top of tussocks without exposing much inter-tussock space where forage was absent.

Eriophorum vaginatum growing in burned plots exhibited higher percentages of crude protein, greater *in vitro* digestibility, and lower levels of lignin than plants growing in unburned plots. It is likely that these differences will persist for only a few years following fire. There was no indication of a similar trend in *Vaccinium vitis-idaea*, another winter-

green species that was common in the study area. Charred lichens had lower percentages of cell solubles and higher levels of lignin than unburned lichens, but the statistical significance of these differences is not known. Caribou appeared to detect and crater for these charred lichens. They seemed to be dead, however, and it is unlikely that they could aid in lichen colonization of burned areas.

There was no evidence that the diet of caribou differed between burned and unburned habitats in either year. They did not modify their diet and forage for post-fire species such as *Epilobium angustifolium*. Forbs and grasses, common on burned areas, only comprised a small percentage of winter diet, and interaction of burn type and use was not significant. Caribou did take advantage of increased availability of *Eriophorum vaginatum* in the burn, but this species is a common component of caribou winter diet in unburned areas as well. Feeding craters were less numerous in burned areas than adjacent unburned areas in 1990, suggesting that although caribou did forage in the burn, it was not desirable habitat.

Fire clearly had a major effect on forage availability. It is important, however, to distinguish between long and short-term effects of fire. Fire killed vegetation that may have eventually inhibited growth of *Eriophorum* tussocks, and it is important in the long-term maintenance of lichen rich tussock-tundra. Lichen availability, however, will be low in the burned area for decades. For the time being, caribou do not appear to be adversely affected by this burn, which is on a migratory route, and seem able to maintain themselves while in the area by subsisting on winter-green vegetation and lichens from unburned islands and adjacent unburned habitat. Large fires occurring on winter range (as opposed to migratory corridors) in close proximity to each other may cause more problems for winter survival of caribou, particularly if the population is near carrying capacity.

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Appendix I. List of plant species encountered in study plots in northwestern Alaska, July 1990-91.

FAMILY	SPECIES
Betulaceae	*Alnus crispa*
	Betula nana
	B. papyrifera
Caryophyllaceae	*Stellaria spp.*
Compositae	*Antennaria* spp.
	Artemesia arctica
	Petasites frigidus
	Senecio congestus
Cyperaceae	*Carex aquatilis*
	C. Bigelowii
	C. membranacea
	C. rariflora
	C. rotundata
	unidentified *C.* spp.
	Eriophorum angustifolium
	E. scheuchzeri
	E. vaginatum
Droseraceae	*Drosera rotundifolia*
Empetraceae	*Empetrum nigrum*
Equisetaceae	*Equisetum arvense*
	E. silvaticum
Ericaceae	*Andromeda polifolia*
	Arctostaphylos alpina
	Chamaedaphne calyculata
	Ledum palustre
	Loiseleuria procumbens
	Oxycoccus microcarpus
	Vaccinium uliginosum
	V. vitis-idaea
Gramineae	*Calamagrostis canadensis*
	Poa arctica
	unidentified grasses
Liliaceae	*Tofieldia pusilla*
Onagraceae	*Epilobium latifolium*
	E. davuricum
Orchidaceae	*Spiranthes Romanzoffiana*
Polemoniaceae	*Polemonium acutiflorum*
Polygonaceae	*Polygonum alaskanum*

Appendix I. (Continued)

FAMILY	SPECIES
Rosaceae	*Potentilla palustris*
	Rubus chamaemorus
	Spiraea Beauverdiana
Rubiaceae	*Galium boreale*
Salicaceae	*Salix planifolia pulchra*
Scrophulariaceae	*Pedicularis sudetica*
Lichens	
	Alectoria spp.
	Cetraria cucullata
	C. islandica
	C. nivalis
	C. pinastri
	Cladina arbuscula
	C. mitis
	C. rangiferina
	C. stellaris
	Cladonia amaurocraea
	C. bellidiflora
	C. botrytes
	C. chloropaea
	C. coccifera
	C. deformis
	C. ecmocyna
	C. fimbriata
	C. furcata
	C. gracilis
	C. metacorallifera
	C. subfurcata
	C. subulata
	C. sulphurina
	C. uncialis
	unknown *C.* spp.
	Hypogymnia physodes
	Icmadophila ericetorum
	Nephroma spp.
	Ochrolechia spp.
	Peltigera spp.
	Sphaerophorus spp.
	Stereocaulon spp.
	unknown lichen spp.

Appendix I. (Continued)

FAMILY	SPECIES
Bryophytes	*Aulacomnium palustre*
	A. turgidum
	Ceratodon purpureus
	Climacium dendroides
	Dicranum spp.
	Distichum spp.
	Hylocomium splendens
	Marchantia polymorpha
	Pholia nutans
	Pleurozium schreberi
	Polytrichum commune
	P. juniperinum
	Ptilium ciliare
	Sphagnum spp.
	unknown liverwort spp.
	unknown moss spp.

Appendix II. Percent of plant fragments[1] identified in caribou fecal samples collected from burned and unburned habitats in late March through April, 1990 and 1991, in northwestern Alaska.

Plant Group	1990 Burned	1990 Unburned	1991 Burned	1991 Unburned
Lichens				
Cladonia, Cladina,				
Peltigera spp.	39.4	42.0	27.5	45.5
Cetraria spp.	16.8	21.5	6.4	7.6
Nephroma spp.	2.1	0.9	3.3	0.3
Total	58.3	64.4	37.2	53.4
Forbs	3.6	2.2	2.5	2.6
Equisetum spp.	NA	1.0	1.3	0.5
Total	3.6	3.2	3.8	3.1
Mosses	12.5	16.7	21.7	18.2
Shrubs				
Andromeda,				
Vaccinium spp.	11.3	1.6	3.2	7.1
Other heath	0.2	1.8	6.4	7.1
Other shrubs	2.0	3.0	3.3	1.6
Total	13.5	6.4	12.9	15.8
Sedges	NA	0.2	1.0	NA
Eriophorum spp.	5.8	2.2	10.7	3.4
Carex spp.	2.1	2.3	9.5	5.2
Total	7.9	4.7	21.2	8.6
Grasses	4.2	4.6	3.2	0.9

[1] Results are not corrected for differential digestion of plant species.

APPENDIX III. Fiber content and *in vitro* digestibility of vegetation collected from caribou feeding craters in burned and unburned plots in northwestern Alaska, late winter 1990 and 1991.

Year=1990

	Fire history[1]		% NDF	% ADF	% ADL	% AIA	*% in vitro* digestibility[2]
Eriophorum vaginatum	B	R1	72.29	32.48	3.97	trace	NA
		R2	77.90	33.96	4.14	trace	NA
	UB	R1	81.36	37.11	4.84	0.01	44.16
		R2	80.57	36.36	4.82	0.06	40.16
Standing dead *Eriophorum vaginatum*	B	R1	84.23	48.56	10.24	trace	19.72
		R2	NA	NA	NA	NA	15.63
	UB	R1	84.83	47.26	9.95	trace	22.47
		R2	NA	NA	NA	NA	26.17
Lichens	B	R1	80.40	12.88	4.88	1.50	9.68
		R2	79.13	10.65	5.70	0.17	13.07
	UB	R1	51.33	10.22	1.47	trace	10.53
		R2	52.55	13.20	1.75	3.00	9.50
Graminoids	B	R1	79.98	45.73	3.43	9.76	48.67
		R2	79.31	45.61	3.65	9.69	48.00
Vaccinium vitis-idaea	UB	R1	33.63	21.92	8.48	0.01	50.14
		R2	32.60	22.31	8.68	0.26	47.32

[1] B=Burned, UB=Unburned, R=lab replicate, S=independent sample.
[2] Cow rumen fluid was used for in vitro digestibility analyses.

APPENDIX III. (Continued)

			Year=1991				
	Fire history[1]		% NDF	% ADF	% ADL	% AIA	% *in vitro* digestibility[2]
Eriophorum vaginatum	B	S1	72.39	33.71	4.12	0.56	51.04
		S2	72.99	32.11	4.75	0.09	48.60
		S3	69.53	32.49	2.71	0.02	58.36
		S4	72.09	32.26	2.72	0.03	54.58
		S5	72.02	33.73	4.50	0.06	46.95
	UB	S1	74.68	37.22	7.06	0.45	44.6
		S2	71.11	37.06	8.00	1.22	43.85
		S3	71.98	35.59	9.64	0.59	42.21
		S4	77.63	36.30	10.81	0.75	40.00
		S5	75.87	38.09	5.71	0.29	42.58
Lichens	UB	S1	31.18	3.48	1.53	0.42	9.97
		S2	34.54	7.35	6.37	0.46	10.95
		S3	39.41	6.19	1.51	0.20	7.60
		S4	46.93	7.61	4.26	1.86	6.85
		S5	44.04	4.06	1.58	0.41	6.64
Vaccinium vitis-idaea	B	S1	40.09	29.87	12.25	2.59	30.43
		S2	43.04	32.16	12.96	2.75	41.32
		S3	41.25	31.25	15.89	2.55	35.27
		S4	37.56	27.96	11.20	2.87	32.25
	UB	S1	41.82	31.92	12.57	2.28	36.52
		S2	43.33	29.87	15.62	2.81	29.21
		S3	38.65	28.10	10.98	2.37	32.74
		S4	42.64	32.68	15.94	2.39	37.88
		S5	41.52	31.97	14.96	3.41	33.98

[1] B=Burned, UB=Unburned, R=lab replicate, S=independent sample.
[2] Cow rumen fluid was used for in vitro digestibility analyses.

APPENDIX IV. Crude protein, crude fat, and gross energy of vegetation collected from caribou feeding craters in burned and unburned plots in northwestern Alaska, late winter 1990 and 1991.

Year=1990

	Fire history[1]		% Crude protein	% Crude fat	Gross energy (calories/g)
Eriophorum vaginatum	B		11.47	1.62	4711.7
	UB		10.28	1.38	4785.6
Standing dead *Eriophorum vaginatum*	B	R1	5.93	1.72	4843.5
		R2	3.68	NA	NA
	UB	R1	4.23	1.61	4789.9
		R2	3.58	NA	NA
Lichens	B	R1	1.77	0.55	4496.6
		R2	1.97	NA	NA
	UB	R1	1.82	3.62	4540.2
		R2	1.96	NA	NA
Graminoids	B	R1	6.63	1.31	4262.6
		R2	6.69	NA	NA
Vaccinium vitis-idaea	UB	R1	4.27	8.59	5409.6
		R2	4.14	NA	NA

[1] B=Burned, UB=Unburned, R=lab replicate, S=independent sample.

APPENDIX IV. (Continued)

Year=1991

	Fire history[1]		% Crude protein	% Crude fat	Gross energy (calories/g)
Eriophorum vaginatum	B	S1	14.07	2.07	4736
		S2	12.03	1.96	4739
		S3	12.60	2.78	4609
		S4	12.45	2.87	4662
		S5	13.06	2.34	5235
	UB	S1	9.43	1.66	4736
		S2	10.13	2.04	4728
		S3	9.92	2.62	4749
		S4	9.12	2.64	4576
		S5	8.56	2.98	4409
Lichens	UB	S1	1.86	5.68	4476
		S2	1.53	5.82	4473
		S3	2.22	5.29	4417
		S4	3.85	4.01	4351
		S5	2.04	6.41	4360
Vaccinium vitis-idaea	B	S1	6.07	6.22	4932
		S2	5.84	6.44	4930
		S3	6.32	7.35	5118
		S4	4.85	9.78	5164
	UB	S1	5.70	7.99	4964
		S2	5.13	7.57	5733
		S3	5.32	10.54	5604
		S4	5.09	8.16	5077
		S5	5.80	7.05	5034

[1] B=Burned, UB=Unburned, R=lab replicate, S=independent sample.